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LA DYNAMIQUE DES ESPÈCES ET DES PEUPLEMENTS APRÈS FEU DANS LA PESSIÈRE DE LA CEINTURE D'ARGILE DU QUÉBEC

THÈSE PRÉSENTÉE COMME EXIGENCE PARTIELLE DU DOCTORAT EN SCIENCES DE L'ENVIRONNEMENT

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AVANT-PROPOS

Quoique seulement un nom apparaît en couverture de cette thèse, les chapitres et annexes de celle-ci sont signés par plusieurs auteurs. Pour satisfaire aux exigences du jury de cette thèse, permettez-moi d'éclaircir le rôle de chacun des auteurs à la réalisation des différents chapitres.

Chapitre 1 : Nicolas Lecomte et Yves Bergeron.
L'initiative scientifique est le fruit de la réflexion de M. Bergeron, les analyses statistiques et la rédaction des articles ont été effectuées par M. Lecomte avec de l'aide de M. Bergeron.

Chapitre 2 : Nicolas Lecomte, Yves Bergeron et Martin Simard.
L'initiative scientifique est venue de M. Bergeron tandis que la conception du design expérimental fut entreprise par M. Lecomte et M. Bergeron. La collecte de données a été faite par M. Lecomte et des aides de terrain. La datation des peuplements a été entrepris par M. Simard et M. Lecomte. Les étapes d'analyses statistiques et de rédaction furent effectuées principalement par M. Lecomte avec l'aide indispensable de M. Simard et M. Bergeron.

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RÉSUMÉ DE LA THÈSE

Se situant dans le cadre d'une démarche qui vise l'instauration d'un aménagement écosystémique, l'objectif principal de l'étude était de décrire les changements de structure et de composition qui se produisent lorsqu'il y a absence prolongée du feu dans la pessière du nord-ouest de l'Abitibi.

À l'échelle du paysage, l'étude démontre que les séries évolutives au sein de ce paysage se retrouvent dans des proportions différentes selon les dépôts de surface. Si nous retrouvons presque exclusivement des peuplements dominés par l'épinette noire (*Picea mariana*) sur dépôt organique, le pin gris (*Pinus banksiana*) domine la canopée de 40% des peuplements jeunes (< 100 ans) sur dépôts grossiers et 10% de ceux-ci sur dépôt fins, tandis que les espèces feuillues (*Populus tremuloides* et *Betula papyrifera*) dominent 20% des peuplements jeunes sur dépôts fins et grossiers. Toutefois, peu importe les dépôts de surface, nos résultats suggèrent que l'absence du feu engendre une convergence vers des peuplements dominés par l'épinette noire. La structure des peuplements au sein de ce paysage est caractérisée par une grande variabilité dans les types de structures de peuplements au sein des jeunes classes d'ages (< 100 ans), qui disparaissent en absence du feu. La baisse en surface terrière et en densité associée à l'absence du feu suggère que nous observons également sur ce territoire une convergence dans la structure des peuplements vers des peuplements ouverts. Par ailleurs, l'abondance sur les différents dépôts de surface des espèces secondaires (*Abies balsamea* et *Larix laricina*) suggère que l'entourbement est un facteur important qui pourrait expliquer la trajectoire des séries évolutives sur les différents dépôts de surface.

Nos résultats démontrent que la composition des arbres après feu (*Pinus* vs *Picea*) a peu d'incidence sur l'accumulation de matière organique au sol, la structure des peuplements ou la composition du sous-bois. Néanmoins, notre étude suggère que la sévérité du dernier feu (épaisseur de la matière organique résiduelle) a des effets considérables sur l'évolution des peuplements. Après un feu sévère (consommation complète de la matière organique), nous observons un recrutement massif de semis qui engendre la formation rapide d'une canopée fermée et d'un sous-bois dominé par les mousses hypnacées. Toutefois, l'absence prolongée du feu (< 100 ans) engendre une

accumulation constante de matière organique au sol, une ouverture de la canopée et un remplacement dans le sous-bois des mousses hypnacées par *Sphagnum* spp et le *Ledum groenlandicum.* Après feu peu sévère (consommation partielle de la matière organique), la dynamique des peuplements se résume par une faible régénération et faible croissance des arbres après feu ce qu'inhibent la fermeture de la canopée, favorisant l'accumulation de la matière organique et un envahissement précoce dans le sous-bois par les *Sphagnum* spp et *L. groenlandicum.* Ainsi, quoique la sévérité du dernier feu engendre une divergence dans les types de peuplements à court terme, l'absence prolongée du feu (<200 ans) engendre une convergence dans la composition et la structure des peuplements résineux sur dépôts fins.

Les résultats de notre étude permettent de questionner l'applicabilité de la Coupe avec Protection de la Régénération et des Sols (CPRS). Les effets des CPRS, qui protègent par définition la matière organique accumulée au sol, ressemblent aux effets des feux peu sévères. Puisque la productivité forestière est significativement réduite après un feu peu sévère en comparaison à celles après un feu sévère, nous préconisons que l'industrie forestière entreprenne des approches sylvicoles qui s'inspirent des effets des feux sévères afin d'assurer le maintien de la productivité forestière et la diversité des types de peuplements après feu au sein de ce paysage. Cela se traduit par l'application d'approches qui 'tuent' la majorité des arbres (coupe totale), éliminent la matière organique accumulée au sol (préparation mécanique, brûlage dirigé, etc.) et qui sont ensuite régénéré à forte densité (plantation à haute densité, 4000-5000 tiges / ha).

INTRODUCTION GÉNÉRALE

0.1 Introduction

Comme en témoigne le Rapport de la Commission Coulombe (2004), l'intérêt pour une foresterie qui s'appuie davantage sur de bonnes connaissances de la dynamique forestière naturelle va croissant depuis quelques années. Cette dynamique naturelle comprend à la fois la variabilité à long terme du régime (fréquence, superficie, sévérité) des perturbations (feu, chablis, épidémie) et l'évolution de la structure et de la composition des peuplements suite aux perturbations. Basé sur le postulat selon lequel les espèces seraient bien adaptées aux forces environnementales sous lesquelles elles ont évoluées au cours des millénaires, on pense sûrement à juste titre qu'un aménagement qui privilégie une composition et une structure des peuplements semblables à celles qui caractérisent les milieux naturels devrait permettre le maintien de la biodiversité et des fonctions essentielles des écosystèmes forestiers (par ex: Macdonald 1995; Bergeron *et al.* 1999). Malgré un intérêt envers ce type d'aménagement, la mise en application de ces concepts n'est pas encore très développée. Au Québec, quoique la loi 136 modifiant *La loi des forêts* (Gouvernement du Québec 2001) permette finalement à l'industrie forestière d'être déroger des normes d'interventions (RNI), en absence d'alternatives concrètes basées sur la dynamique forestière, l'industrie forestière et le ministère hésitent à s'éloigner des pratiques traditionnelles usuelles.

Le développement d'une stratégie d'aménagement forestier s'inspirant de la dynamique forestière naturelle comprend trois étapes (Bergeron et Harvey 1997). La première consiste de reconstituer le régime des perturbations naturelles; la deuxième vise l'étude de l'évolution à long terme de la structure et de la composition des peuplements suite aux perturbations. La dernière étape consiste à développer des interventions sylvicoles qui ressemblent à la dynamique naturelle des perturbations. Ces interventions n'ont pas pour but de 'mimer' la dynamique naturelle mais bien de préserver les processus écosystémiques clefs et la mosaïque naturelle des écosystèmes au sein du paysage. Ce projet de doctorat vise à documenter la deuxième étape de cette mise en pratique. L'objectif principal est de décrire l'évolution à long terme de la structure et de la

composition des peuplements issus de feux et d'élucider les mécanismes qui induisent cette évolution au sein du domaine de la pessière de l'Ouest.

0.2 Dynamique forestière en forêt boréale

Les capacités régénératrices des espèces (liées au feu : cônes sérotineux ou semi-sérotineux, système racinaire résistant au feu) favorisent une composition après feu similaire à celle avant feu (Heinselman 1981). Avec un cycle de feu plus court que la longévité des espèces, la dynamique forestière se réduit à comprendre le comportement du feu qui agit comme un filtre d'une génération d'arbre à une autre (Johnson 1992). Cette dynamique est un exemple du modèle de succession parallèle (*sensu* Frelich and Reich 1995) qui a souvent été attribué à la forêt boréale pour expliquer la rétention des multiples trajectoires après feu et l'empêchement des peuplements d'atteindre l'équilibre (climax) (Carleton and Maycock 1978)

Toutefois, des études réalisées en forêt boréale au cours des deux dernières décennies ont démontré le lien entre les changements temporels et spatiaux du climat et la fréquence du feu (Bergeron et al. 2004a, Flannigan et al. 1999). Des études rétrospectives dans l'Est de l'Amérique du Nord ont démontré que la forêt boréale serait, depuis la fin du 'Petit Âge Glaciaire' (1850), influencée par des feux de moins en moins fréquents (Bergeron et al. 2004a). La diminution de la fréquence des feux en forêt boréale à conifères du Nord-ouest de l'Abitibi a comme conséquence le fait qu'une majorité des peuplements (57%) au sein de ce paysage n'ont pas brûlés depuis au moins 100 ans (Gauthier et al. 2000). Par ailleurs, les conditions climatiques en forêt boréale ne favorisent pas la décomposition ce qui entraîne, en absence du feu, une accumulation de matière organique au sol qui peut dépasser un mètre de profondeur à certains endroits (Boudreault et al. 2002, Taylor et al. 1987). Les incendies forestiers, surtout lorsqu'ils s'étendent sur de grandes superficies et brûlent sur plus d'une journée, peuvent, tout en causant la mortalité des arbres, présenter des variations dans l'épaisseur de la matière organique résiduelle au sol laissé sur leur parcours (Nguyen-Xuan *et al.* 2000, Brais et al., 2000). Loin de représenter un effet marginal, cette matière organique résiduelle, en altérant la disponibilité des espèces (Moore and Wein 1977) et les lits de germination,

influence à court terme la diversité et la quantité de la régénération (Chrisoweicz 1974; 1976; Zasada *et al.* 1983; Rydgren *et al.* 2004; Nguyen-Xuan *et al.* 2000) ainsi que la croissance des arbres (Zasada *et al.* 1987). Par contre, à notre connaissance, aucune étude n'a démontré comment ces effets évoluent à travers le temps en comparant à long terme la dynamique des peuplements en fonction de la sévérité du dernier feu.

Le modèle de la succession parallèle a été généralement accepté en forêt boréale (e. g. Johnson 1992) car peu d'études ont étudié la dynamique forestière à long terme; la longévité du maintien des différentes espèces qui dominent la canopée après feu est donc peu connue (Larsen and Macdonald 1999). Puisque le régime de feu est fonction du changement global du climat, il importe de connaître la chronologie de la dynamique des peuplements issus de feu de sévérité variable à de longues échelles temporelles. Ces connaissances de la forêt boréale à conifères permettront d'améliorer la modélisation des effets écologiques associés au changement global du climat. Cette modélisation pourrait permettre de rendre notre mitigation de ces impacts plus efficaces et, couplée avec des études sur la croissance des peuplements à travers le temps, éclairera le rôle futur ('source' ou 'puits'?) de la forêt boréale à conifères dans le cycle global du carbone.

0.3 Approche

Pour obtenir une image globale de l'effet de l'absence du feu sur la structure et la composition des peuplements au sein de ce paysage, nous nous sommes servi (chapitre 1) des inventaires temporaires du Ministère des Ressources Naturelles (Saucier 1994). En superposant cet inventaire sur une carte des feux (Bergeron et al. 2004b), nous avons inféré les trajectoires successionelles en combinant l'approche dite de 'chronoséquence' à l'étude de la distribution verticale (hauteur des arbres) des espèces au sein des peuplements. Cette étude nous a permis de comparer les trajectoires et l'abondance relative des séries évolutives sur les différents dépôts présents sur ce territoire. De plus, étant donné que les dépôts de surface possèdent différents potentiels d'entourbement, la comparaison de la succession entre les dépôts nous permet d'élucider les effets de l'entourbement sur les trajectoires des séries évolutives.

Le deuxième volet de cette étude a été consacré à la dynamique des peuplements résineux occupant des stations hydrique-mésique sur dépôts à texture fine puisque des études à l'échelle du paysage démontrent que ces types de peuplements occupent la majorité de la partie forestière de ce paysage (Harper et al. 2002, Bergeron et al. 2004). Avec la carte des feux du territoire, nous avons délimité une cinquantaine de peuplements sur des conditions abiotiques similaires (pente, drainage) qui incorporent la gamme d'âge, et de structure des peuplements résineux au sein de ce paysage. Pour combler certaines lacunes associées à l'approche chronoséquence, nous avons greffé à notre étude des analyses paléoécologiques qui nous ont permis de déterminer la composition initiale des peuplements et d'obtenir un aperçu de la sévérité du dernier feu. En absence du feu en forêt boréale, les conditions climatiques défavorables à la décomposition entraînent une accumulation de matière organique au sol. La stratigraphie de cette matière organique qui s'est accumulée en entassant annuellement des fragments de végétaux plus au moins décomposés représente un enregistrement de l'évolution de la composition des peuplements à travers le temps (Foster 1985). Ce phénomène nous a permis d'étudier les changements de composition qui ont eu lieu depuis le dernier feu dans chaque site. Ainsi, nous avons pu vérifier si l'étude de peuplements d'âges variables (chronoséquence) au sein de ce paysage représente les changements qui ont lieu au sein d'un site en absence de feu.

En suivant cette approche , nous avons dans un premier temps étudié comment l'absence du feu, la composition initiale et la sévérité du dernier feu influencent la structure des peuplements (chapitre 2). En deuxième lieu, nous avons analysé la façon dont ces facteurs affectent l'accumulation de matière organique (chapitre 3). Finalement, nous avons décrit comment ces facteurs influencent la composition du sous bois (chapitre 4).

0.4 Hypothèses

Nous formulons l'hypothèse selon laquelle la diversité de structure et de composition des peuplements au sein du domaine de la pessière à mousse de l'Ouest est due à la variabilité de la sévérité du feu ainsi qu'aux processus opérant à l'échelle du

peuplement en absence du feu. Nous proposons que l'absence du feu engendre 1) un remplacement d'espèces dans la canopée qui s'explique par la tolérance des espèces à l'ombrage de même que par l'entourbement; 2) une ouverture de la canopée qui est produite par des perturbations secondaires et maintenue par une perte de productivité entraînée par l'entourbement et 3) un remplacement dans le sous-bois des mousses hypnacées par les sphaignes et les arbustes éricacées. Par ailleurs, puisque la présence de matière organique résiduelle après feu influence la quantité et la croissance à court terme de la régénération (Chrisowiecz 1974; 1976, Zasada 1983, 1987), nous proposons qu'à long terme les peuplements issus de feux peu sévères demeurent ouverts tout au long de la succession avec un envahissement précoce des espèces de sous-bois intolérantes à l'ombre (*Sphagnum* spp et *L. groenlandicum*).

1

CHAPITRE I

Successional pathways on different surficial deposits in the coniferous boreal forest of the Quebec Clay-Belt.

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1.1 Abstract

To infer successional pathways on different surficial deposits in north-western Quebec, we combined the chronosequence approach to the study of within-stand species and stem vertical distributions. The surficial deposits sustained not only different frequencies of post-fire stand composition types, but also different successional trajectories. After fire, *Picea mariana* BSP (Mill.) dominated all stands on organic deposits while shade intolerant species dominated the canopy in over 30% and 60% of stands on respectively fine-and coarse-textured deposits. In the absence of fire, *P. mariana* eventually dominates the canopy of all stands on every surficial deposits. However, as the frequency of *Larix laricina* (DuRoil) K.Kock, and *Abies balsamea* (L.) Mill. in old stands (> 100 years) are respectively positively and negatively correlated with the paludification potential of the surficial deposits, changes in composition in this landscape appear to be driven by the species' tolerance to shade and paludification. Structural changes were characterised by the gradual replacement of closed dense stands by open stands, which coincided with changes in canopy composition. However the comparison of young and old *P. mariana* dominated stands suggests that in this landscape structural changes may occur in the absence of changes in composition. The high structural diversity of *P. mariana* dominated stands within the youngest age classes suggests that other fire regime parameters, a part from time since fire, may also explain the diversity of stand structures within this landscape. Given the diversity of successional pathways under similar abiotic conditions, it appears that in the coniferous boreal forest a prediction model of forest structure and composition must include not only the recent temporal dimension but also the qualification of fire behaviour parameters.

1.2 Résumé

Pour inférer les trajectoires successionelles dans le nord-ouest du Québec, nous avons combiné l'approche dite de 'chronoséquence' à l'étude de la distribution verticale, au sein des peuplements, des tiges et des espèces. Les dépôts de surface contrôlent non seulement des fréquences différentes de composition après feu mais aussi des trajectoires successionelles différentes. Après feu, *Picea mariana* BSP (Mill.) domine tous les

peuplements sur dépôts fins tandis que des espèces intolérantes à l'ombre dominent la canopé de 30% et 60% des peuplements sur respectivement les dépôts à texture fine et grossière. En absence de feu, *P. mariana* domine la canopée de tous les peuplement sur chacun des dépots de surface. Toutefois, puisque la fréquence de *Larix laricina* (DuRoi) K.Kock, et *Abies balsamea* (L.) Mill sont respectivement positivement et négativement reliées avec le potentiel d'entourbement des dépôts de surface, les changements de composition au sein de ce paysage sont déterminés par la tolérance des espèces à l'ombre et l'entourbement. Les changements de structure des peuplements, qui se charactérisent par un remplacement des peuplements denses et fermés par des peuplements ouverts, coincident avec les changements de composition. Par contre, en comparant la structure des jeunes et vieux peuplements dominés par *P. mariana*, nos résultats indiquent que des changements de structure en absence du feu peuvent avoir lieu même sans changement dans la composition. Au sein des jeunes classes d'âge, la variabilité de la structure des peuplements dominées par *P. mariana* suggèrent que d'autres paramètres du feu en dehors du temps écoulé depuis le dernier feu pourraient être important pour expliquer la diversité de structure des peuplements au sein de ce paysage. Étant donné la diversité de séries évolutives dans des conditions abiotiques similaires, un modèle de la dynamique forestière au sein du domaine de la pessière à mousse devrait inclure non seulement la dimension temporelle récente mais aussi la qualification des paramètres liés au comportement des feux.

1.3 Introduction

The view of boreal forest dynamics has gradually shifted in recent decades. Many studies had suggested that the high fire frequency in the boreal forest, coupled to the high similarity between pre and post-fire stand compositions, inhibited directional succession to occur and that succession therefore tended to be cyclical (Dix and Swan 1971, Johnson 1992). However, in the past two decades, independent reports have indicated a high spatial and temporal variability in fire frequency within the Canadian boreal forest (Bergeron et al. 2004a, Flannigan et al. 2001).

Associated to the fire reconstruction studies, chronosequence, permanent plot and careful stand reconstruction studies have indicated that in the prolonged absence of fire, species replacement can occur, notably the replacement of *Pinus* species and deciduous species by shade-tolerant *Picea* and *Abies* species (Carleton and Maycock 1978, Frelich and Reich 1995, Lesieur et al. 2002). This pattern of succession has been postulated to be mainly driven by minor disturbances at the scale of single trees (insect / fungal attack, windthrow), which gradually chisel away at the even-structured closed stands which typically arise after large disturbances such as fire. These small-scale gap processes engender changes in stand composition by favouring shade-tolerant species, which are already established in the understory (Bergeron 2000).

As forest dynamics become progressively influenced by small gap processes, stand structural development leads to the evolution of even-structured stands into uneven-structured stands (Kneeshaw and Burton 1997, Kneeshaw and Bergeron 1998, Bergeron 2000). Structural development is usually associated to the above-mentioned changes in composition, which result in the taller early successional species being replaced by the shorter shade-tolerant species. However, in the eastern Canadian boreal forest, *P. mariana*, a shade-tolerant species, by producing serotinous cones can form monospecific post-fire stands (Harper et al. 2002, Dix and Swan 1971). Given that *P. mariana* can regenerate abundantly by seed and layering under a conspecific canopy, stand structural changes can occur without species replacement (Groot and Horton 1994, Harper et al. 2002).

In the northern part of the boreal forest, a process known as paludification which involves a build-up of organic matter may be important in explaining changes in stand composition and structure. While the causes of paludification include the creation of a water-saturated environment characterised by low temperature, decreased microbial activity, and decreased availability of important nutrients, notably N and P (Heinselman 1981, Van Cleve and Viereck 1981, Taylor et al. 1987). Since some species are able to persist under this unfavourable environmental regime, while many others exhibit decreased vigour and annual growth, the process of paludification may be important in determining stand successional direction. Furthermore paludification may also affect the structural development of stands. In some boreal regions, small scale gaps are hastily

closed by the growth of shade-tolerant coniferous species from the understory into the canopy (Kneeshaw and Bergeron 1998, Bergeron 2000) which maintains the canopy of stands relatively closed (Kneeshaw and Burton 1997). However in regions where paludification is an important process, the degradation of site quality induced by paludification (Heinselman 1963; Glebov and Kurzukhin 1992), may hinder the capacity of tree saplings to grow and hence close the canopy. Since paludification is related to the water holding capacity of the underlying surficial deposit (Prescott et al. 2000), the comparison of successional pathways among the main surficial deposits should yield some insight if the process of paludification exhibits a bottom-up control of successional trajectories in this landscape.

Given the presumed interaction between surficial deposits and successional processes, improved knowledge of natural succession on the different surficial deposits should ameliorate the prediction of the composition and structure of forest stands that would characterise the natural landscape under different fire cycles. To improve our knowledge of succession for this part of the boreal biome, we combine the chronosequence approach to the study of within-stand diameter distribution to infer future developmental stages. Although both methods have been critiqued in the literature, we believe our approach of combining these techniques and using a large data set (over 750 stands) partially overcomes their respective shortcomings.

We hypothesised that in the absence of fire 1) species and individual replacement in the canopy can occur in this part of the boreal forest and is driven by the individual species' shade and paludification tolerance and 2) as a result of the combined effects of disturbances other than fire and paludification, even structured closed stands that characterise young successional stages will as succession proceeds develop and maintain an open canopy and uneven structured diameter distribution.

1.4 Methods

1.4.1 Study area

The study area (49°N to 51° 20'N; 78° 30'W to 79° 50'W) is located within the Clay Belt of northwestern Quebec, Canada and is within the *Picea mariana*—

feathermoss bioclimatic domain (Robitaille and Saucier 1998). The Clay Belt is a physiographic unit composed mostly of clay deposits left by pro-glacial Lake Ojibway; organic soils and glaciofluvial deposits are also common. (Veillette 1994), Although a few rocky outcrops are scattered across the landscape, the topography is generally flat. Average annual temperature (1971-2000) recorded at the closest weather station to the North (Matagami, 49° 43'N, 77° 37'W) and to the South (La Sarre, 48° 46'N, 79° 13'W) of the study area are respectively –0.6 ° C and 0.8 ° C with an average of 857 mm and 905 mm of precipitation annually (Environment Canada 2005). Most of the area is dominated by *P. mariana,* which forms monospecific, structurally diverse stands, while occasional deciduous and pine-dominated stands are dispersed across the landscape (Harper et al. 2002). Fire cycle length has increased from 101 years before 1850, to 398 years since 1920; mean stand age is 148 years (Bergeron et al. 2004b).

1.4.2 Databases

The Quebec Ministry of Natural Resources (QMNR) gathered the data used to describe successional changes. Since the QMNR inventories the forest for forestry purposes, forest stands on slopes of more than 40% (rare in the study area) and with a canopy shorter than < 7 m were not sampled. In the study area, 953 circular plots of 400 m^2 were sampled either in 1987, 1989 or 1996. The plots were sampled every 250 m along 1.5 km transects. In each 400 m^2, every tree with a diameter > 10 cm was identified to species and tabulated in 2-cm diameter classes, and in a concentric subplot of 40 m^2, trees with diameters < 10 cm were measured in the same manner. Additionally, in each plot the age at breast height of three dominant trees was measured. With an eco-forestry database, we divided the stands into four surficial deposit types (thin, coarse, fine and organic) a 4 slope types (0-3%, 4-8%, 9-15%, 16-30%) and 5 canopy closure classes (0-20%, 20-40%, 40-60%, 60-80% > 80%) (similar to those being established by the Quebec provincial forest inventory program, Harper et al. 2002). By overlaying fire reconstruction maps (Bergeron et al. 2004b) onto the forest inventory, we assigned a date since last fire to every forest stand by validating the fire map date with the oldest age determined for the three dominant trees aged per stand. The fire reconstruction maps

were developed by dating post-fire tree cohorts for fires before 1880, and using archives and aerial photographs for fires after 1880 (Bergeron et al. 2004b).

Overall we were able to confidently attribute a surficial deposit type, a slope class and a time since fire date to 797 stands (Appendix 1.A). Due to an insufficient number of stands we have excluded young stands (< 50 years, 4 stands) and stands on thin soils (12 stands). As compared to previous landscape scale studies in this area (Bergeron et al. 2004b, Harper et al. 2002), the forestry inventory data set, with respect to surficial deposits and stand age, appears to be representative of the forested portion of the landscape under study (Appendix 1.A).

1.4.3 Data analyses

1.4.3.1Ordination

To obtain an integrated representation of the forest tree composition and to evaluate the factors responsible for the variation in composition, a Canonical Correspondence Analysis (CCA) was computed using the relative abundance of each species (% of total basal area) ((CANOCO Version 4, (Ter Braak and Šmilauer 1999)). The environmental variables (time since fire, surficial deposit, slope class) were loaded by forward selection. Significance of each variable was computed using a Monte Carlo test ($\alpha = 0.05$). The downloading option was used for rare species. As the CCA with all the stands demonstrated that surficial deposit was an important factor in determining stand composition, separate CCA's were computed for each surficial deposits.

1.4.3.2 Age-class classification

In order to investigate changes in stand composition and structure in relation to time since last fire (TSF) we divided our stands into 4 age-classes (50-100, 100-150, 150-200 and 200+). To investigate seedling / sapling bank recruitment in the prolonged absence of fire, we calculated for each surficial deposit the proportion of stands older than 100 years where each species was present in the diameter classes < 9cm.

1.4.3.3 Within stand canopy-advanced regeneration trends

To assess canopy – advanced regeneration (canopy-regen) relations within stands, we subdivided the trees in the stands into either canopy trees or advanced regeneration trees. As previous studies have demonstrated that canopy height decreases in the absence

of fire (Harper et al. 2002), we have chosen an alternative method to the traditional static forestry definition of advanced regeneration (i.e. trees smaller than a certain diameter). To accomplish the canopy-regen division, we firstly subdivided the trees into 6 diameter classes (0-4.9 cm, 5-8.9 cm, 9-12.9 cm, 13-16.9 cm, 17-20.9 cm and > 21 cm). Secondly, to determine where the canopy-regen boundary would be set between these diameter classes, we established that this boundary, starting with the largest diameter class and moving down, would be set when the cumulative surface area was at least 20% of the total stand basal area. The '20% boundary' was chosen as on average the largest diameter class (< 21cm) made up 20 % of the total stand basal area. Given our procedure and due to the variability in stand structure, we have obtained 5 different canopy-regen types, which differ in the location of their respective canopy-regen delimitation. For the majority of stands (> 98%), we have excluded the smallest diameter class due to their associated high mortality rates. However in a few very old (> 200 years) or young stands (50 - 100 years), trees > 10 cm did not make up 20 % of the total stand basal area, for these stands the advanced regeneration is solely trees with a diameter < 5cm. To assess canopy-regen relations within stands, for each surficial deposit and for each species dominating in the canopy, we calculated the proportion of stands were each species was present or dominated the advanced regeneration.

1.4.3.4 Stand structural development

Stand structural development was assessed by calculating for each age-class the average and coefficient of variation of each of the following six variables: 1) diversity of diameter classes (Shannon's index), 2) coefficient of skewness for diameter, 3) mean diameter (cm), 4) density (stems/ha), 5) surface area (m^2/ha) and 6) volume. To investigate if structural changes or within age-class stand structural variability could be due to the variability in surficial deposit, stand composition or slope, we isolated stands where *P. mariana* dominated in the canopy and in the advanced regeneration. We then compared how the structural attributes varied between the surficial deposits and between the two main slope classes (0-3% and 3-8%) on fine-textured deposits.

1.5 Results

1.5.1 General ordination trends

Our CCA with all stands demonstrated that 1) the canonical axis 1 and axis 2 explained respectively 20% and 4 % of the variance in species composition, and 2) time-since-fire explained 14% of the variation, surficial deposit 9% and slope 1 %. The total inertia of the individual CCA's for each surficial deposit indicate that stands on coarse deposits display the highest variability in species composition and ones on organic the least (Table 1.1). For all surficial deposits time-since-fire was again the most important explanatory variable. The ordination diagram with all the stands revealed that 1) time since last fire is negatively correlated with axis 1 and positively correlated with axis 2, 2) that the differentiation as to surficial deposit is a significant factor, with sites on coarse-textured deposits on the upper right side of the ordination diagram and sites on organic and fine-textured deposits negatively correlated with axis 1 (Fig. 1.1a). The position of *P. mariana* near the centre indicates that this species is present on all substrates regardless of the age of the stand. The position of *Pinus banksiana* Lamb., *Betula papyrifera* March. and *Picea glauca* (Moench) Voss. in the upper right of the ordination diagram indicates their early successional status and/or preference for coarse-textured deposits. The position of *Populus tremuloides* Michx. in the lower-right of the ordination diagram demonstrates its early successional status and preference for fine-textured deposits. The intermediate positive position of *Abies balsamea* (L.) Mill. on axis 1 and its positive position on axis 2 indicate that it is associated with long fire intervals on coarse-textured deposits. *Larix laricina* (DuRoil) K.Kock, being positioned in the lower left corner of the ordination diagram indicates its preference for fine-textured and organic deposits. The size and position of the age-class 80% confidence ellipses for each surficial deposit suggests that the absence of fire induces a converging decrease in stand composition diversity (Fig. 1.1bcd).

1.5.2 Age-class classification trends.

On organic deposits apart from two young stands, *P. mariana* dominates the total and canopy stand basal area in all age-classes (Fig. 1.2). In the older stands, excluding *P.mariana*, only *L. laricina* occasionally dominates the advanced regeneration. On fine-textured deposits, while *P mariana* dominates the canopy, advanced regeneration and

overall basal area of nearly all the stands older than 100yrs, *P. tremuloides* and *P. banksiana* dominate the canopy basal area of about 30% of the youngest stands. On coarse-textured deposits shade-intolerant species, dominate the canopy basal area of over half of the stands within the youngest age-class. While *P.mariana* dominates the canopy of all the oldest stands, *A balsamea* dominates the total and advanced regeneration basal area of 25% of the stands older than 200 years.

On organic and fine-textured soils the frequencies of small *P.mariana* and *L. laricina* stems increase as the time since last fire increases while the frequency of small *A. balsamea* stems appears to decrease or stabilise (Table 1.2). On coarse-textured deposits, only small *A. balsamea* and *P. mariana* stems are present in the prolonged absence of fire and the frequencies of small stems of these species increases as the time since last fire increases (Table 1.2). Small *P. tremuloides* and *P. glauca* stems were encountered respectively in only two and one stand older than 100 years (data not shown).

1.5.3 Within stand canopy-advanced regeneration trends

When *P. mariana* dominates in the canopy numerous species can be present in the advanced regeneration, however conspecific stems or occasionally *A. balsamea/P. glauca* on coarse-textured deposits and *L. laricina* on fine and organic textured deposits, dominate the advanced regeneration (Table 1.3). When deciduous species (*P. tremuloides* and *B. papyrifera*) dominate in the canopy the advanced regeneration is mainly composed of conspecific, *P.mariana* or *A. balsamea/P. glauca* stems. While conspecific or *P. mariana* stems tend to dominate the advanced regeneration in the youngest age-class, the older age-classes on fine-textured deposits are almost exclusively dominated by *P.mariana* with a few stands by *A. balsamea/P. glauca* (Fig. 1.2,Table 1.3). On coarse-textured soils the older deciduous dominated canopies tend to be preferentially dominated by *A. balsamea/P. glauca* than *P.mariana*. When *P. banksiana* dominates in the canopy, in the youngest age-class the advanced regeneration is either dominated by conspecific stems or more commonly *P. mariana* stems and in the older age-classes almost exclusively dominated by *P. mariana* (Fig. 1.2, Table 1.3).

1.5.4 Successional trends in stand structure for the main surficial deposits.

A part from a decrease in stand density little structural changes were observed on organic soils (Fig. 1.3). On coarse and fine-textured deposits the 6 stand structural attributes varied as follows. Stand density decreased after 100 years and remained relatively constant afterwards; stand basal area remained constant between 50 and 150 years since the last fire and decreased afterwards; stand volume and mean diameter increased to eventually decrease after 150 years; the diversity of diameter classes remained relatively constant through time and finally stand coefficient of skewness for diameter remained relatively low for the first 150 years to subsequently increase (Fig. 1.3). The same trends in structural attributes were apparent when we isolated stands where *P. mariana* dominated the canopy and advanced regeneration basal area (data not shown).

Although our date set comprises more old stands than young stands (Appendix 1.A), on all deposits, the within age-class coefficients of variation for the 6 structural attributes tended to be higher in stands younger than 150 years as compared to stands older than 150 years (Fig. 1.4). This higher structural variability among stands in the youngest age-class was also observed when we looked solely at *P. mariana* dominated stands and when we compared the structural development of *P. mariana* dominated stands on fine-textured deposits on the two main slope classes (Fig. 1.4). Similarly, on coarse and fine-textured deposits, while about 40 % of the stands in the youngest age-classes have closed canopies (>60% cover), over 90% of the canopies of older stands are open (<60% cover) (Table 1.4). Little changes in canopy closure were observed on organic deposits with over 90 % of stands exhibiting less than 60% cover (Table 1.4).

1.6 Discussion

1.6.1 Successional pathways within the study area on different surficial deposits

Within the study area, as *P. tremuloides, B. papyrifera, P. mariana* and *P. banksiana* may be the dominant species following fire numerous successional pathways co-occur under similar abiotic conditions. However, the comparison of successional pathways on the different surficial deposits, revealed significant differences in the

relative abundance of the respective pathways and different trajectories of the post-fire stands (Figure 1.5).

While *P. mariana* dominates on organic deposits, the other successional pathways are encountered on coarse and fine-textured deposits. The relative abundance of the *P. banksiana* and *B. papyrifera* successional pathways are more abundant on coarse-textured deposits while the *P.mariana* and *P. tremuloides* pathways are more abundant on fine-textured deposits. The difference in relative importance of the successional pathways occurring on the deposits might be due to different disturbance regimes among the surficial deposits types. Paleoecological studies south of the study area, have demonstrated that high fire frequencies favour *P. banksiana* and *B. papyrifera* over *P.mariana* (Larocque et al. 2000). While Bergeron et al. (2004) found that fire frequencies were lower on organic soils than fine and coarse-textured deposits, no significant difference in fire interval length was observed between these two latter deposit types (Appendix 1.A). Nonetheless recent radiocarbon datings of forest floor humus accumulated just above the uppermost charcoal in stands on fine-textured deposits, revealed that the dendroecological dates obtained for sites older than 200 years significantly underestimated the age of some stand (Cyr et al. 2005). This suggests that fire frequency on fine-textured deposits may in fact be lower than the one on coarse-textured deposits, which may explain the different relative abundance of successional pathways occurring on fine and coarse-textured deposits.

Alternatively the differing paludification potentials of the surficial deposits may influence fire severity which in turn may influence the relative abundance of the successional pathways. For a given fire interval and stand composition, stands on fine-textured deposits will tend to have more organic matter accumulated on the ground as compared to coarse-textured deposits. Given a fire of equal intensity, this fire is more likely to not fully remove the organic matter accumulated above the fine-textured deposits. Low severity fires that do not remove all the organic matter would favour species that do not require an exposed mineral seed bed to germinate, such as *P. mariana* (Jeglum et al. 1979) and unlike *P. banksiana* (Lavoie and Sirois 1998). Furthermore, it has been argued that the fire resistant reproductive organs of the two dominant deciduous species may differ as to their capacity to survive fires of differing severity. It has been

postulated that *B. papyrifera* which resprouts from the stem collar would be more resistant to high severity fires than *P. tremuloides* that resprouts from roots (Viereck 1983). Therefore a fire regime at the scale of the Holocene composed of more frequent fires and/or fires of greater severity on coarse-textured soils as opposed to fine textured deposits may explain the different relative importance of the successional pathways on these deposits.

As *P. mariana* dominated all old stands and the advanced regeneration of most stands, succession in this landscape appears to be driven by the shade tolerance of the species. Shade-tolerant species in the absence of fire would be able to progressively invade and survive in the understory and would be at a competitive advantage when the fire cohort is dismissed by secondary disturbances (Frelich and Reich 1995, Bergeron 2000). However, since the frequencies of *A. balsamea* and *L. laricina* in later stages on the three surficial deposits were respectively negatively and positively correlated to the paludification potential of these deposit, the species tolerance to paludification appears be an important factor driving succession in the coniferous boreal forest. On coarse-textured deposits *P. mariana* stands and the deciduous dominated stands are more likely to evolve towards *A. balsamea* co-dominated stands as compared to stands on fine-textured deposits (Figure 1.5). While, on organic and fine-textured deposits *P. mariana* stands are more likely to be invaded by *L. laricina* than stands on coarse-textured deposits. We propose that the higher paludification potential of fine-textured and organic deposits favours *L. laricina*, which is known to tolerate nutrient poor conditions (Heinselman 1981, Van Cleve and Viereck 1981, Giroux et al. 2001). While the low paludification potential of coarse-textured deposits as compared to finer textured deposits, favours *A. balsamea* over *P.mariana.* This hypothesis is supported by studies that have shown that on coarse-textured deposits no significant difference in the growth rates of *A. balsamea* and *P. mariana* regeneration was observed 10 years after the removal of canopy trees (Doucet and Boily 1995), while on more paludified sites *P. mariana* had significant better growth rates than *A. balsamea* (Brumelis and Carleton 1988).

1.6.2 Structural development pathways

Stand structural development coincided with changes in species composition, however the same structural development pathways were apparent when comparing young and old *P. mariana* dominated stands. Stand structural development in our study area, at first glance, appear to mirror those of the biomass accumulation model and the stand development stages of respectively Borman and Likens (1979) and Oliver and Larson (1996). Early stages are dense and of low volume, intermediate stands of lower density and higher volume while older stands are characterised by lower volume, as the fire origin cohort is replaced by understory trees. Paludification appears to be prevalent within our study area, as old stands tend to be characterised by low volume, open canopies and a high within stand coefficient of skewness for diameter. As stands become paludified and the fire origin cohort is dismissed the variability in the microtopography is likely to increase with the formation of a hummock / hollow pattern that will gradually characterise old stands. Heterogeneity of microsites has a major influence on growth variation and hence size inequality in *P. mariana* stands (Macdonald and Yin, 1999). Furthermore, since older stands tend to be more open than young stands and there exists a positive correlation between the openness of a stand and the potential windthrow risk hazard (Smith et al. 1987), the openness of the canopy may also be maintained by a high rate of windthrow induced gap formation. Regardless of the causes, the low variability among stands within the oldest age class suggests that as succession proceeds, canopy closure rate falls below the rate of canopy gap formation which maintains the canopy of old stands very open.

1.6.3 Convergence of parallel structural development pathways

The high variability among *P. mariana* stands within the younger age-classes as compared to older age-classes for the structural attributes studied, suggest that multiple converging structural development pathways may be present within our study area. While it has been generally accepted that post-fire tree regeneration is high in the boreal forest, some have shown that stands exhibiting initial differences in tree densities have followed different recovery pathways (Arsenault 2001, Johnstone et al. 2004). Furthermore, some authors have described 3 natural disturbance histories that may lead to poor post-fire tree

regeneration in *P. mariana* stands. Some have indicated that a short fire interval may engender a poor post-fire tree regeneration (Lavoie and Sirois 1998, Larocque et al 2000, Payette 1992). Others have demonstrated that regeneration may be low if a fire occurs in a *P. mariana* dominated stand having recently been affected by a spruce budworm outbreak (Payette et al. 2000). Finally, Foster (1985) suggested that a fire of low severity that does not fully consume the organic matter accumulated above the mineral soil may, by lowering the availability of adequate seedbeds, engender a low post-fire regeneration

Although we cannot completely rule out other factors, given the low fire frequency in this landscape (Bergeron et al. 2004a) combined with the process of paludification (Boudreault et al. 2002), we propose that the variability in fire severity may be the chief process which explains the high variability in stand structure within young successional stages. This hypothesis clearly necessitates further study however it is corroborated by two recent studies, which looked at the stratigraphy of the organic matter accumulated above the mineral soil. These studies found, in sparsely regenerated young stands (<100 years), charcoal horizons within the organic matter, as opposed to one horizon just above the mineral soil in similarly-aged densely regenerated stands (Cyr et al. 2005; N. Lecomte uppl data).

1.7 Conclusions

Given the processes and patterns described, we conclude that within our study area as stated by Noble and Slatyer (1980) succession is led by processes acting at the population level and can be predicted by the vital attributes of the species. Given the occurrence of paludification and a fire regime characterised by large and infrequent fires, within the coniferous boreal forest of north-western Quebec, the key species vital attributes driving succession are their ability to reinvade burns, their shade tolerance, as well as their tolerance to paludified conditions.

The forest mosaic in this landscape is composed of a diversity of stand types, which can be partially explained by the absence of fire and the underlying surficial deposit. In order to maintain this diversity, forest management regimes should vary the proportions of successional series on the different surficial deposits and should, without

abandoning clear cuts, introduce partial cuts to mimic successional changes occurring in the absence of fire. Furthermore, given the prevalence of paludification in this landscape, certain sylvicultural interventions that physically remove the organic matter accumulated above the mineral soil may be necessary, in order to counteract the detrimental effects of paludifcation on tree productivity.

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Table 1.1

Summary statistics of the four canonical correspondence analyses using a forward selection of environmental variables.

Surficial deposit	Total inertia of CCA	% of variance explained by time since last fire	% of variance explained by surficial deposit	% of variance explained by slope
All	1.9	14	9	1
Coarse	2.1	11		0
Fine	1.65	12		5
Organic	0.2	0		0

Table 1.2

Proportion of stands with small stems (DBH < 9cm) of P. mariana, A. balsamea and L. laricina per surficial deposit and 50 year time since fire (TSF) age class older than 100 years

	Surficial deposit								
	Organic			Fine			Coarse		
	TSF (years)			TSF (years)			TSF (years)		
Species	100	100-150	> 200	100	100-150	> 200	100	100-150	> 200
P. mariana	100.0	90.8	98.6	86.3	96.4	97.8	80.0	88.2	100.0
A. balsamea	12.5	6.2	8.2	21.6	24.1	17.8	20.0	35.3	37.5
L. laricina	0.0	23.1	19.2	2.0	8.9	12.4	0.0	0.0	0.0

Table 1.3

Canopy – advanced regeneration relationships. Frequency of stands where the different species or group of species is present (a) and dominates (b) the advanced regeneration depending on surficial deposit and the species that dominates in the canopy.

(a) Species present in the advanced regeneration	Species dominating in the canopy (# of stands)								
	PTR + BPA			PBA			PMA		
	organic (0)	fine (46)	coarse (10)	organic (0)	fine (22)	coarse (41)	organic (154)	fine (432)	coarse (71)
PTR + BPA		80	100		32	15	1	6	12
PBA		22	10		95	93	1	1	24
PMA		78	70		95	95	100	100	98
PGL + ABA		30	60		14	5	17	25	23
LLA		4			5		14	5	

(b) Species dominating in the advanced regeneration	Species dominating in the canopy (# of stands)								
	PTR + BPA			PBA			PMA		
	organic (0)	fine (46)	coarse (10)	organic (0)	fine (22)	coarse (41)	organic (154)	fine (432)	coarse (71)
PTR + BPA		24	60						
PBA					50	40			4
PMA		67	10		45	60	99	99	98
PGL + ABA		9	30						7
LLA					5		<1	<1	

Table 1.4

Relative importance of open and closed stands with respect to surficial deposit (organic, fine and coarse) and time since fire (TSF) (T1 (<100 yrs), T2 (100-200 yrs) and T3 (200+ yrs)) with (a) all stands and (b) P. mariana dominated stands.

(a) All stands	Surficial deposit								
	Organic			Fine			Coarse		
	TSF			TSF			TSF		
Stand canopy types	T1	T2	T3	T1	T2	T3	T1	T2	T3
Closed (density>60%)	0	14	4	50	36	10	38	15	0
Open (density<60%)	100	86	96	50	64	90	62	85	100

(b) *P. mariana* dominated stands	Surficial deposit								
	Organic			Fine			Coarse		
	TSF			TSF			TSF		
Stand canopy types	T1	T2	T3	T1	T2	T3	T1	T2	T3
Closed (density>60%)	0	14	4	39	35	10	39	9	0
Open (density<60%)	100	86	96	61	65	90	61	91	100

1.10 Figure captions:

Figure 1.1: Canonical Correspondence Analysis of the tree composition (relative abundance of basal area). a). tree species and explanatory variables. Stands are regrouped by surficial deposit (b. organic, c. fine and d. coarse) and represented as age class 80% confidence ellipses, light dash (50-100 years), dark dash (100-150 years), light line (150-200 years) and dark line (>200 years) (due to the similarity of the age class ellipses, stands on organic soils are represented as one ellipse). Vectors represent a connection of the age class ellipse centroids going from youngest to oldest. Species codes are as follows: aba, Abies balsamea; bpa Betula papyrifera; lla Larix laricina; pba, Pinus banksiana: pgl, Picea glauca; pma, Picea mariana; ptr, Populus tremuloides. Environmental variables are as follows: TSF, time since last fire; coarse, centroid of stands on coarse-textured deposits; organic, centroid of stands on organic deposits; S1, centroid of stands on slopes between 0-3%; S2, centroid of stands on slopes between 3-8%.

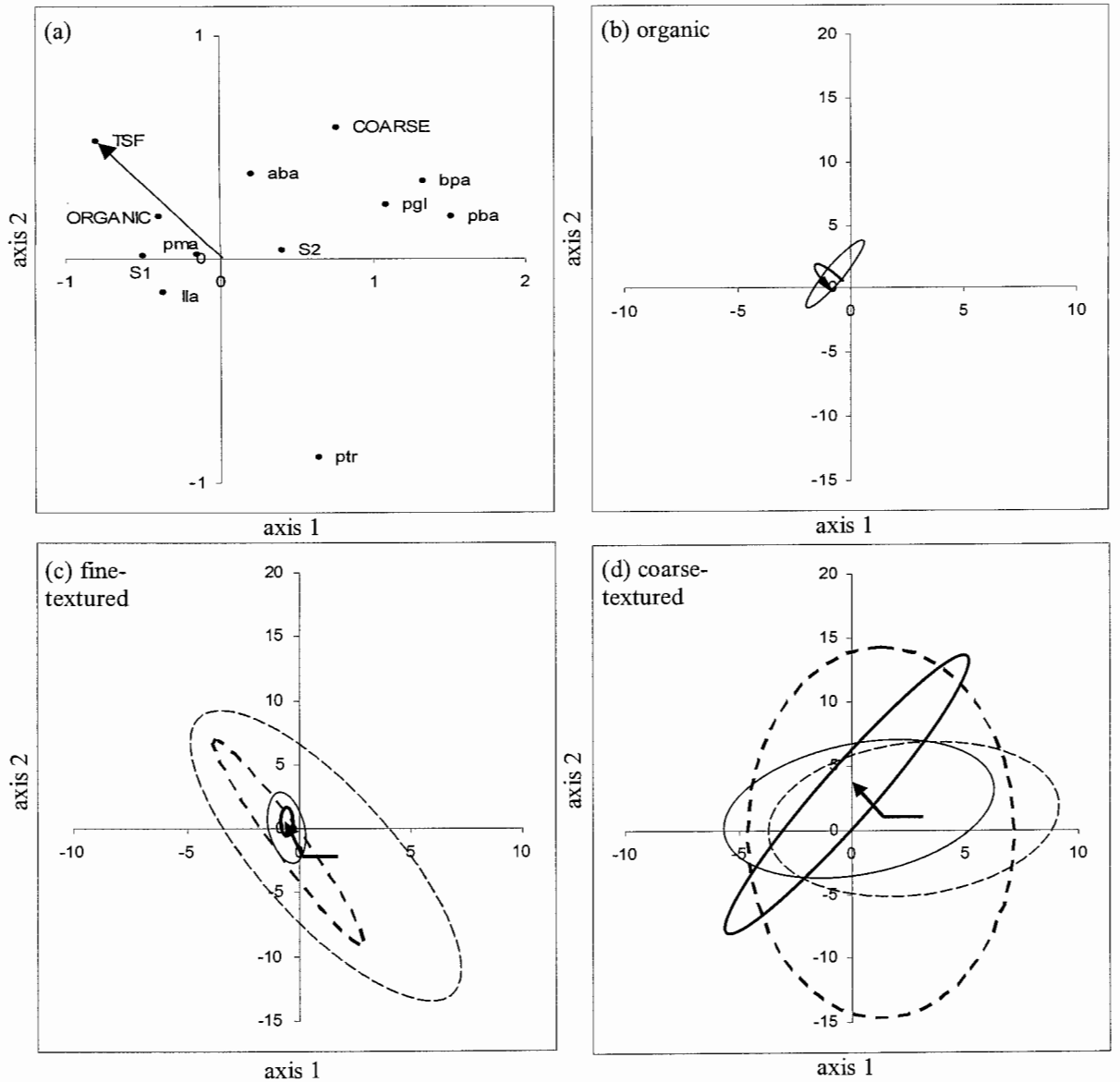
Figure 1.2: Proportion of stands where each species is dominating the total, canopy and advanced regeneration basal area, per 50 yr age class, .for each surficial deposit (a) organic, (b) fine-textured and (c) coarse-textured (for species codes see figure 2).

Figure 1.3 : Mean and associated coefficient of variation values obtained for the 6 structural attributes (stand density, basal area, volume and mean diameter; coefficient of skewness, and Shannon's diversity index for dbh) per 50 yr age class and per surficial deposit.

Figure 1.4 : Mean of the within age-class coefficient of variation values obtained for the 6 structural attributes used in our study (stand density, basal area, volume and mean diameter; coefficient of skewness, and Shannon's diversity index for dbh) per 50 yr age class and per surficial deposit for (a) all stands and (b) stands where P. mariana dominates the canopy and advanced regeneration basal area and (c) P. mariana dominated stands on fine textured deposits on the two main slope classes (slope 1: 0-3% and slope 2: 3-8%).

Figure 1.5: Successional pathways in the coniferous boreal forest of northwestern Québec on different surficial deposits as inferred by this study. Proportion of each forest type after fire and in the extended absence of fire are also shown.* Deciduous species (P. tremuloides and B. papyrifera)

1 **Figure 1.1**


(a)
TSF
COARSE
aba
bpa
pgl
pba
ORGANIC
pma
S2
S1
lla
ptr
axis 2
axis 1
(b) organic
axis 2
axis 1
(c) fine-textured
axis 2
axis 1
(d) coarse-textured
axis 2
axis 1

2

Figure 1.2

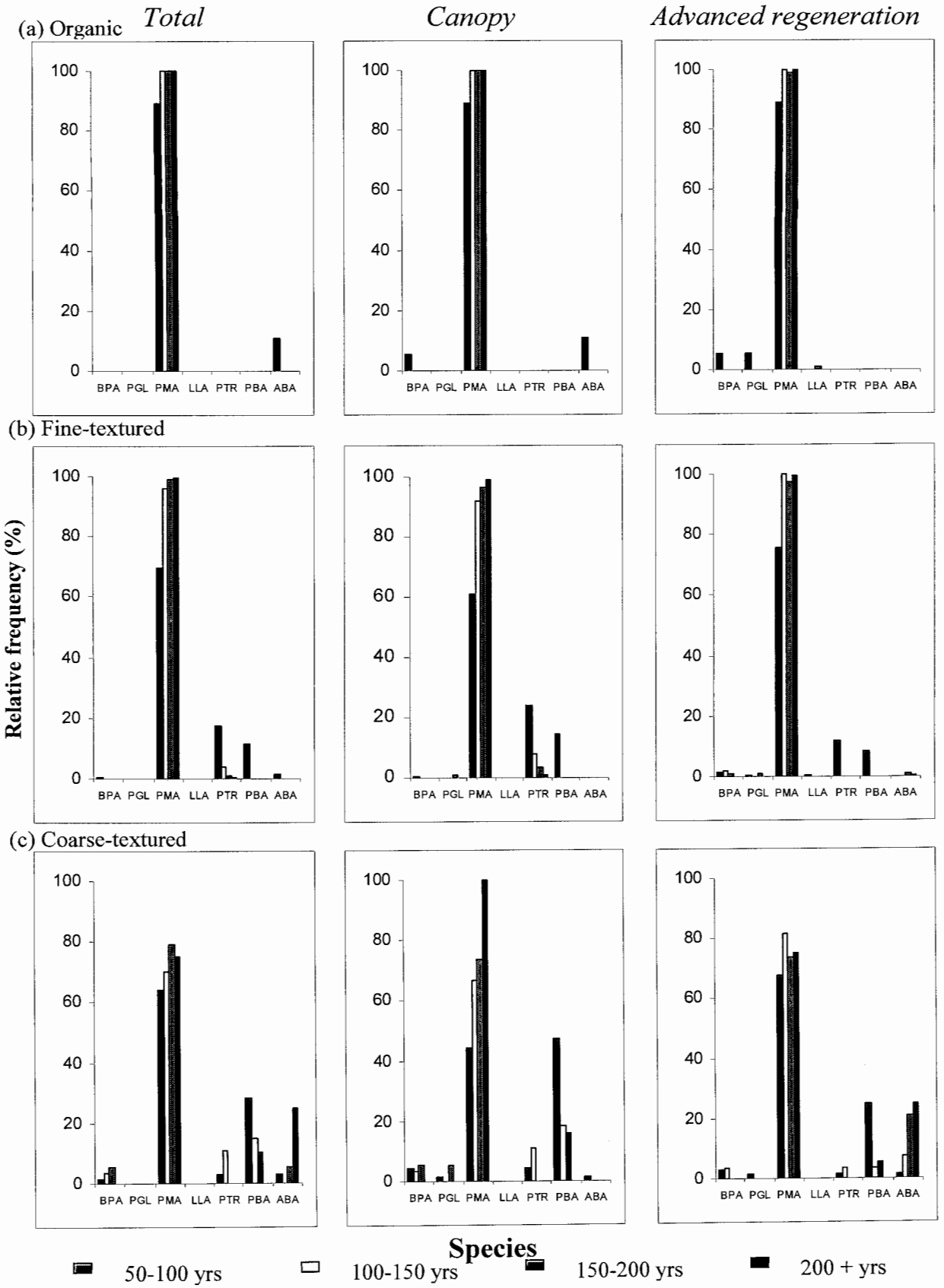

(a) Organic
Total
Canopy
Advanced regeneration
(b) Fine-textured
(c) Coarse-textured
Relative frequency (%)
100
80
60
40
20
0
BPA PGL PMA LLA PTR PBA ABA
Species
50-100 yrs
100-150 yrs
150-200 yrs
200 + yrs

Figure 1.3

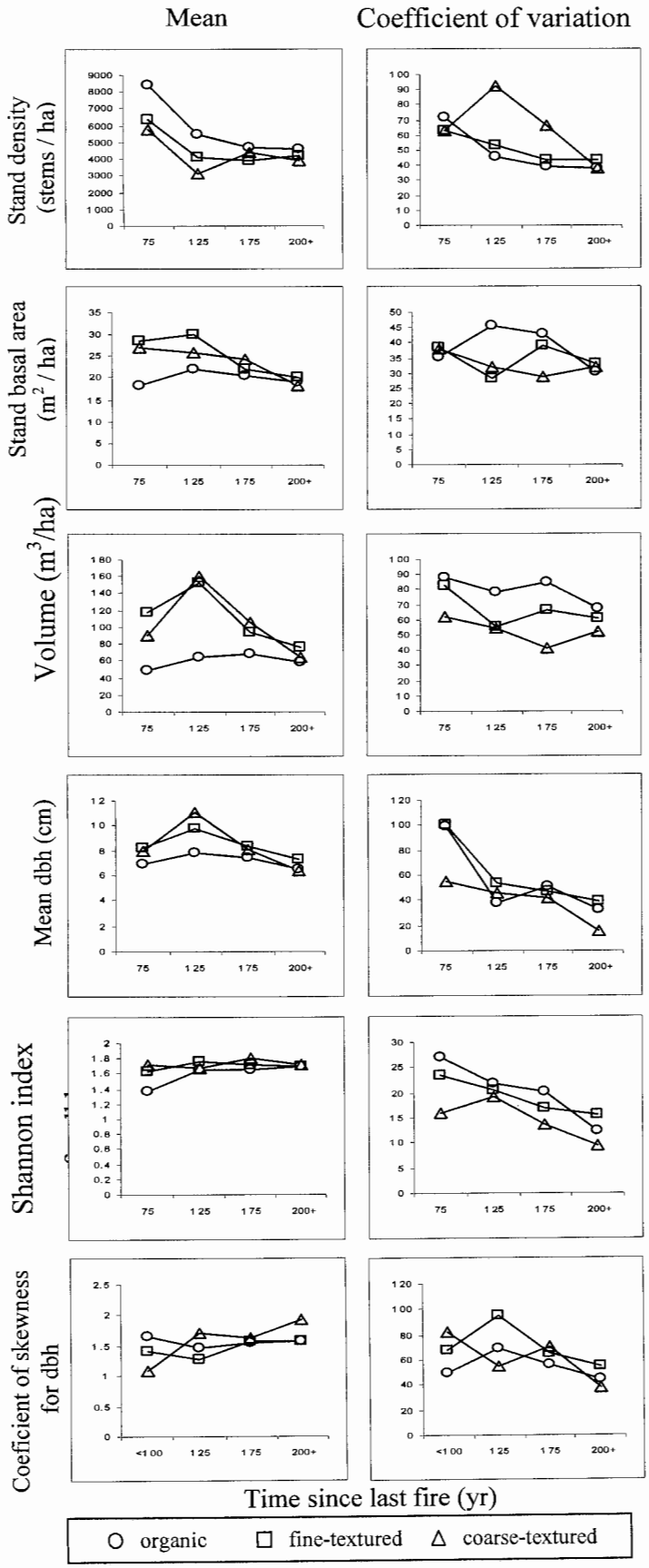
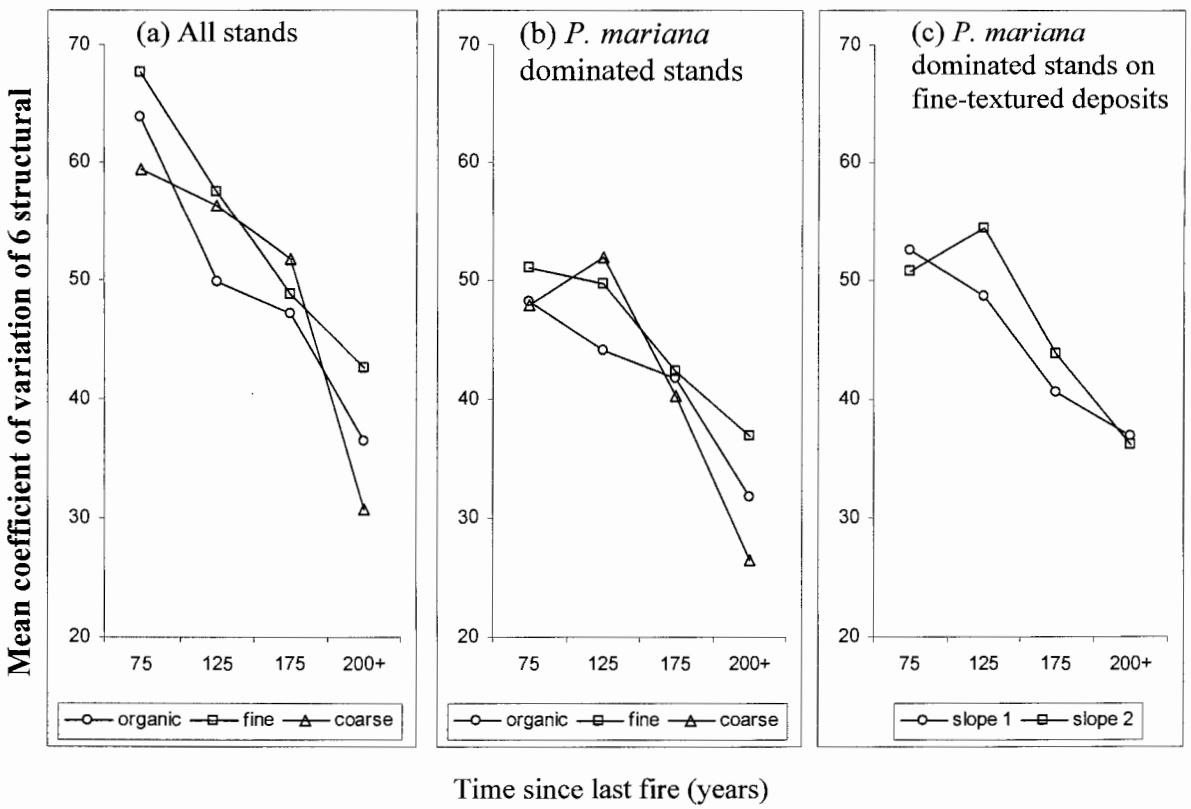
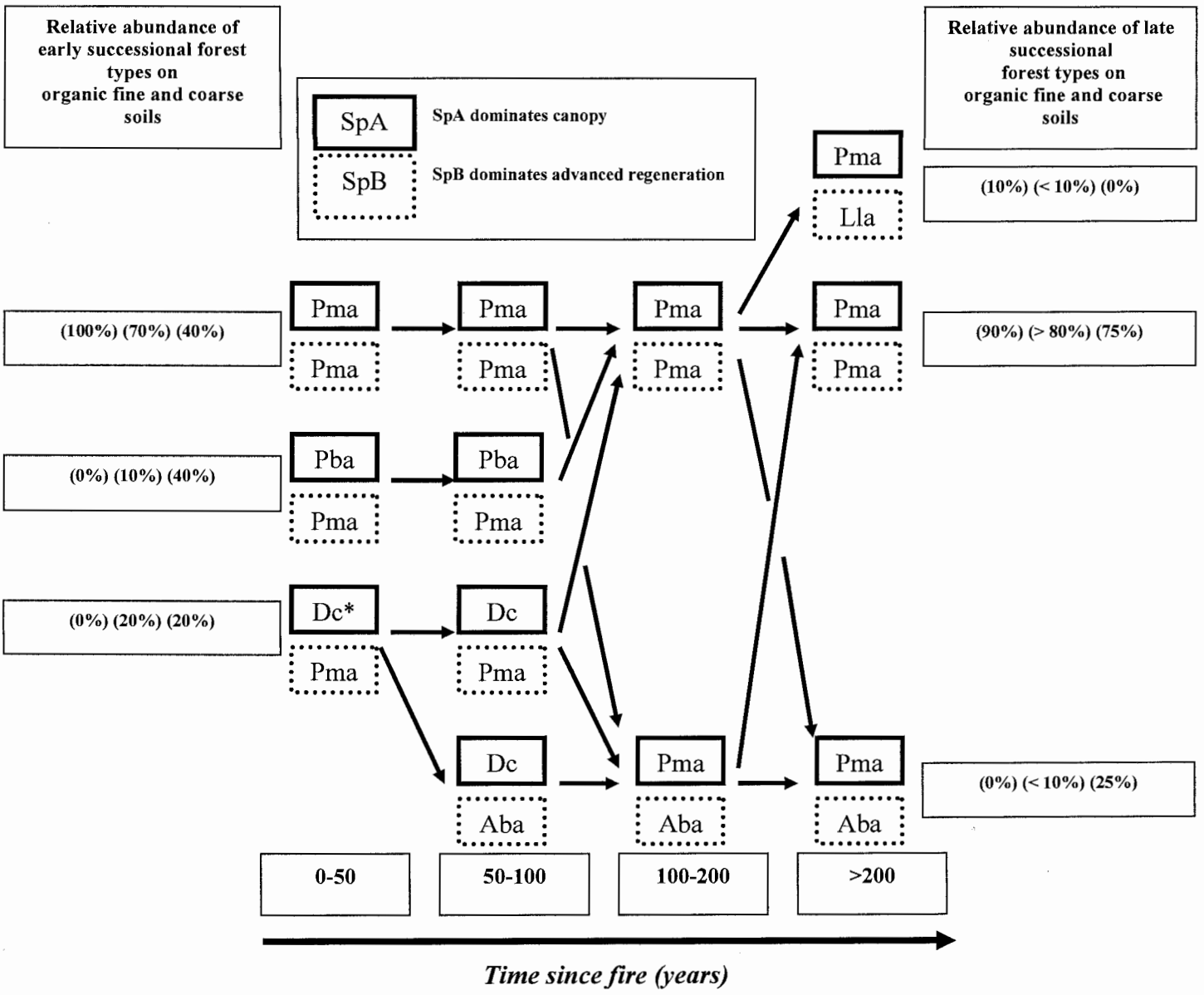

Mean
Coefficient of variation
Stand density (stems / ha)
Stand basal area (m^2 / ha)
Volume (m^3/ha)
Mean dbh (cm)
Shannon index
Coeficient of skewness for dbh
75
125
175
200+
<100
Time since last fire (yr)
organic
fine-textured
coarse-textured

Figure 1.4


Mean coefficient of variation of 6 structural
(a) All stands
(b) P. mariana dominated stands
(c) P. mariana dominated stands on fine-textured deposits
70
60
50
40
30
20
75
125
175
200+
organic
fine
coarse
slope 1
slope 2
Time since last fire (years)

1 **Figure 1.5**

2
3
4
5



Appendix 1.A.

Distribution of the 781 stands under study with respect to surficial deposit and time since fire age class. Representatively of the 781 stands with respect to the relative abundance (% cover) of surficial deposits and mean stand age on each surficial deposit as compared to two previous landscape studies (Bergeron et al. 2004b; Harper et al. 2002).

	Time since fire (years)					% cover		Mean stand age (yrs)	
Surficial deposit	50-100	100-150	150-200	>200	Total	our study	Harper et al. 2002	our study	Bergeron et al. 2004b
Coarse	71	27	19	8	125	16	12	108	104
Fine	151	52	111	187	501	64	66	156	134-147
Organic	9	8	65	73	155	20	22	188	151
All	231	87	195	268	781	-	-	154	148

CHAPITRE II

Effects of fire severity and initial tree composition on stand structural development in the coniferous boreal forest of northwestern Quebec, Canada

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2.1 Abstract

The effects of fire severity and initial post-fire tree composition on long-term stand structural development were investigated in the *Picea mariana*-feathermoss bioclimatic domain of northwestern Quebec. Paleoecological methods were used to categorize the severity of the last fire (high or low) and initial tree composition (*Picea mariana* vs. *Pinus banksiana*). Changes in stand structure were evaluated by quantifying stand structural attributes along three chronosequences. Except for accelerating stand break-up, the post-fire presence of *P. banksiana* (which is eventually replaced by *P. mariana*) had little effect on stand structural development. Fire severity had significant effects on the evolution of stand structural attributes, with low severity fires being particularly detrimental for stand productivity. Stands colonizing low severity fires were characterized by low post-fire tree recruitment and growth, and remained open throughout succession. In contrast, after high severity fires, dense productive stands were rapidly established regardless of tree composition, and gradually became open as succession proceeded. These results suggest that in the prolonged absence of fire, the different stand structural development pathways gradually converge regardless of fire severity or initial composition. We argue that stand structural diversity within the coniferous boreal forest is a result of the severity of the last fire and of processes operating at the stand scale in the absence of fire.

Keywords: black spruce (*Picea mariana*), chronosequence, Clay Belt, forest succession, jack pine (*Pinus banksiana*), natural disturbances, residual soil organic matter, stand structure.

2.2 Résumé

Les effets de la sévérité du dernier feu et de la composition forestière post-incendiaire initiale sur le développement à long terme de la structure des peuplements ont été étudiés dans le domaine de la pessière noire à mousses de l'Ouest du Québec. Des méthodes paléoécologiques ont été utilisées afin de catégoriser la sévérité du dernier feu (forte versus faible) et la composition initiale (*Picea mariana* versus *Pinus banksiana*). Les changements dans la structure des peuplements ont été évalués en quantifiant des attributs de structure le long de trois chronoséquences. Si la présence après feu de *Pinus banksiana* (qui est éventuellement remplacé par *P. mariana*) a accéléré le bris des peuplements, elle a eu peu d'effets sur l'évolution de leur structure. Cependant, la sévérité du dernier feu a significativement influencé l'évolution des attributs structuraux des peuplements, les feux peu sévères étant particulièrement néfastes pour la productivité des peuplements. Les peuplements qui tirent leur origine d'un brûlis peu sévère sont caractérisés par une faible régénération, une faible croissance après feu et une canopée qui est maintenue ouverte tout au long de la succession. Après un feu sévère, peu importe la composition après feu, on observe au contraire une installation rapide d'un peuplement dense et productif qui s'ouvre graduellement en l'absence prolongée du feu. Ces résultats suggèrent donc que les différentes trajectoires de développement de la structure des peuplements convergent graduellement, et cela peu importe la sévérité du dernier feu ou la composition initiale. Nous avançons que la diversité dans la structure des peuplements au sein de la forêt boréale conifèrienne est fonction de la sévérité du dernier feu et de processus opérant en l'absence du feu.

Mots-clés: ceinture d'argile, chronoséquence, épinette noire (*Picea mariana*), matière organique résiduelle du sol, perturbations naturelles, pin gris (*Pinus banksiana*), structure des peuplements, succession forestière.

Nomenclature : Marie-Victorin, 1995 for vascular plants; Anderson *et al.*, 1990 for bryophytes; Poole & Gentili, 1996-97 for insects.

2.3 Introduction

Maintaining the diversity of forest structure types at the landscape scale is thought to be crucial for the conservation of species diversity (Lindenmayer & Franklin, 2002). Therefore, a better understanding of the factors influencing the structural development of forests is essential to achieve sustainable forest management. In boreal regions that are under the influence of short fire cycles (< 100 y), changes in tree composition or stand structure are rarely observed between two fire events (Johnson, 1992). In contrast, in the eastern boreal forest of North America, where the cool humid maritime climate currently induces much longer fire cycles (> 300 y; Foster, 1985; Bergeron *et al.,* 2004a), forest succession and stand structural changes can occur (Groot & Horton, 1994; Bergeron, 2000; Harper *et al.*, 2002; 2005).

In the boreal forest, even under similar abiotic conditions, multiple successional trajectories in overstory tree composition can co-occur within a landscape (Harper *et al.* 2002). This co-occurrence can be strongly linked to site-specific historical fire regimes (Payette, 1992; Johnstone & Chapin, *in press*). Short fire intervals tend to favor tree species that reach sexual maturity quickly such as *Pinus banksiana*, whereas longer fire cycles tend to favor longer-lived species or species that are able to regenerate in the absence of fire such as *Picea mariana.* Long fire cycles also result in a high proportion of low severity fires that do not fully consume the thick forest floor that has accumulated during the long fire-free intervals (Foster 1985; Simon & Schwab 2005).

Studies undertaken in the Clay Belt of Ontario and Quebec have shown that virtually all stands that have not burned in 200 y are open forests with discontinuous canopies (Boudreault *et al.,* 2002; Harper *et al.*, 2002). However, these studies have also demonstrated that the structural variability among stands is very high 50 y after fire, with only about half of the stands exhibiting > 60% canopy cover (Harper *et al.*, 2002; Lecomte & Bergeron, 2005, Chap1). These results suggest a high among-stand diversity the early post-fire structural development. In this study, we investigate the influence of fire severity and initial tree composition on stand structural development in the Clay Belt of Ontario and Quebec. We refer to fire severity exclusively as the effects of fire on the accumulated soil organic matter (quantity of duff burned / quantity of duff unburned

sensu Miyanishi & Johnson, 2002) as opposed to the effects of fire on the canopy (% trees killed; *sensu* Greene *et al.*, 2004).

We suggest that among-stand structural diversity in eastern boreal landscapes can be explained by processes operating at the stand scale in the absence of fire and also by initial post-fire stand conditions. Since mixed stands are composed of two species, with one shade-tolerant and long lived (*Picea mariana*) and the other shade-intolerant and short lived (*Pinus banksiana*), we hypothesize that the presence of *P. banksiana* will result in an a bi-modal within-stand vertical distribution of stems as oppossed to a uni-modal distribution in the pure *P. mariana* stands. Furthermore, given that *P. banksiana* is a faster growing and shorter lived species than *P. mariana*, we hypothesize that the co-dominance of *P. banksiana* will result in a higher stand productivity but a premature and quicker rate of stand break-up. Although few studies have examined the long-term effects of fire severity on stand structural development, short term studies indicate that post-fire tree germination and subsequent growth are negatively impacted by an increase in residual duff depth (Chrosciewicz, 1976; Zasada *et al.*, 1983; 1987; Charron & Greene, 2002). We thus hypothesize that stands evolving after low severity fires will be more open and will exhibit reduced tree productivity as compared to stands established after high severity fires.

2.4 Methods

2.4.1 Study Area

The study area (49°00' - 50°00' N; 78°30' - 80°00' W) is located in the eastern North American coniferous boreal forest and is within the *Picea mariana*—feathermoss bioclimatic domain (Robitaille & Saucier, 1998). This area is on the Clay Belt of northeastern Ontario and northwestern Quebec, a physiographic unit composed mostly of clay deposits left by pro-glacial Lake Ojibway (Veillette, 1994). While a few rocky outcrops are scattered across the landscape, the topography is generally flat. Average annual temperature (1971-2000) recorded at the closest weather station to the North (Matagami, 49° 46'N, 77° 49'W) and to the south (La Sarre, 48° 46'N, 79° 13'W) are respectively –0.7 °C and 0.7 °C with an average of 906 mm and 890 mm of precipitation

annually (Environment Canada, 2005). The area is dominated by *P. mariana,* which tends to form monospecific, structurally diverse stands (Boudreault *et al.*, 2002; Harper *et al.*, 2002; 2005). Occasional deciduous- and pine-dominated stands are dispersed across the landscape. Fire is the main disturbance that terminates and initiates secondary succession. Fire cycle length has increased from 101 y before 1850 to 398 y since 1920; mean stand age is 148 y (Bergeron *et al.*, 2004b).The spruce budworm (*Choristoneura fumiferana*) has a small impact in this area compared to regions further east and south. Both historical patterns of budworm defoliation (Boulet *et al.*, 1996; Gray *et al.,* 2000) and tree-ring reconstructions (M. Simard, N. Lecomte, and Y. Bergeron, *unpublished data*) show that spruce budworm is a negligible disturbance factor in these black spruce-dominated forests.

2.4.2 Chronosequence Dataset

2.4.2.1 Site Selection And tree Sampling

During the summers of 2000-2002, using a stand initiation map developed for the northern part of the Clay Belt (Bergeron *et al.,* 2004b), we visited all the burned areas that were located < 2 km from a road. In all, 43 distinct fires of different age were sampled. In each fire, the density and composition of the post-fire tree cohort (*P. mariana* vs. *P. banksiana*) was estimated based on live and/or dead tree composition. Within each fire, at least one representative 10 m x 10 m quadrat was placed for detailed dendroecological analysis. When variable post-fire density or composition was observed within the same fire, several quadrats were sampled. As a result, a total of 48 sites were sampled within 43 distinct fires. Each site had to be on fine-textured mineral deposits, on a slight incline, and free of any sign of anthropogenic disturbance. In each quadrat for each tree species, the height and dbh (diameter at breast height) of all live and dead stems > 2 m in height were measured. Dead trees buried under the organic matter were exhumed, measured and identified to species based on bark, branching and wood morphology. Origin of dead stems (pre- or post-fire) was assessed with the presence / absence of charcoal. Saplings (trees < 2 m in height) were sampled in a randomly selected sub-quadrat. As we attempted to roughly sample the same number of saplings as

the number of trees, the size of this sub-quadrat varied with the density of trees and saplings.

2.4.2.2 Stand Age Determination

Stand age (fire year) for the youngest stands (< 100 y old) was determined from a stand initiation map (Bergeron et al. 2004b) and was validated by counting rings from cross-sections taken at the base of dominant trees (n = 3 to 20). In older stands, stand age was obtained by carefully dating cross-sections taken at the base of live and dead dominant trees (n = 3 to 20). Cross-sections were finely sanded and crossdated using a frost-ring chronology, under a dissecting microscope at 40x magnification. Crossdating was verified using the program COFECHA (Holmes, 1983). In stands where the oldest tree was older than 200 y, and where no fire scars nor pioneer species (*P. banksiana*) were found, samples of carbonized plant remains found in the uppermost charcoal layer in the soil humus were sent to IsoTrace Laboratory (Toronto, Ontario) for AMS (accelerator mass spectrometry) radiocarbon dating. The radiocarbon years were calibrated in calendar years using INTCAL98 (Stuiver *et al.*, 1998; Appendix 2.A). Radiocarbon datings from a parallel study on two of the old stands (Cyr *et al.*, 2005) are also shown (Appendix 2.A). In this study however the authors dated the organic matter located just above the uppermost charcoal layer within the humus profile, which may account for the slightly younger dates obtained as compared to our radiocarbon dates from carbonized material. Nonetheless, since in both cases the age of humus predates the age of the oldest tree present in the stand, we have used the radiocarbon dates from carbonized plant remains.

2.4.2.3 Soil Texture And Topography

Although the mineral soil texture was hand-checked *in situ*, at each site, two mineral soil samples were taken at the center of the quadrat, one at the surface and another at a depth of 1 m. Soil texture was then determined with the Bouyoucos hydrometer method (McKeague, 1976). The mineral soil topography, which may be masked by peat accumulation, was assessed with a theodolite at each site along four 50-m transects each starting at the center of the quadrat and passing through one of the corners.

Significance of the slopes were assessed with simple linear regressions and non-significant slopes ($P > 0.05$) were given a value of zero. If the slopes of transects going in opposite directions were of opposite signs, or if one or both of the slopes was null, we calculated the slope of the two transects combined (*i.e.*, one transect of 100 m). If the slopes were of the same sign, we summed these slopes to obtain a negative slope value (depression) or positive value (mound or incline) for the 100 m transect. The slope index used in this study is the mean of the slopes of the two 100 m transects.

2.4.2.4 Fire Severity

At each stand, the soil burn severity of the last fire was qualified as being either high (HS) or low (LS) based on the quantity of duff that was not consumed by the last fire (*i.e.*, the residual organic matter). Ideally soil burn severity is quantified as the amount of organic matter consumed (*sensu* Myanishi & Johnson, 2002). Nonetheless, as it is impossible to know how much organic matter was present in the pre-fire stand, we have chosen to qualify fire severity as the amount of organic matter not consumed by the fire (*sensu* Nguyen-Xuan *et al.,* 2000). The residual organic matter was measured with two methods: first, by detailed laboratory analysis of a few humus profiles per site, and second, by *in situ* observations of charcoal layers in numerous pits and trenches dug into the humus layer. At each site, between 2 and 4, 10 cm x 10 cm monoliths of the organic layer were cut down to the mineral soil with a Wardenaar sampler. The monoliths were frozen and then sliced into 1-cm thick sections. Subsamples of 50 cm^3 were defloculated in a 2% NaOH solution for 24 h at 60 °C before a gentle manual water spray was used to sieve the samples through a 2 mm mesh. Samples were then bleached in a 10 - 20% HCl solution and identified microscopically at 40x magnification. The percentage of mineral soil was estimated, and charcoal fragments were extracted, dried and then weighed. The mineral soil / organic matter interface for each monolith was established where the mineral soil represented less than 25% of the particles retained in the 2 mm mesh. The depth of the residual organic matter was calculated as the number of 1-cm thick layers above the mineral soil but under the last charcoal layer deposited.

In the younger black spruce sites (< 150 y), 2.25-m trenches were dug about 20 cm into the mineral soil. At every 15 cm along the trenches, the depth of the uppermost

charcoal layer and of the mineral soil were noted, so that the thickness of the residual organic matter could be calculated. Additionally, in each *P. banksiana* and *P. mariana* stand, respectively 10 and 15, 25 x 25 cm pits were dug into the mineral soil every 2 m along two or three randomly chosen 10-m transects. For each pit, the same measurements were noted as done for the trenches.

2.4.2.5 Site classification

The substitution of time by space (chronosequence approach) to understand long-term stand dynamics has been widely used but also extensively criticized. The main potential drawback of using a chronosequence approach is the possibility of selecting stands that differ with respect to their biophysical site characteristics and/or initial conditions after the stand-replacing disturbance. We carefully selected and characterized the biophysical conditions of stands to reduce variability in surficial deposit and slope (Appendix 2.A). Furthermore, we are confident that the paleological methods used in this study (exhumation and identification of dead wood, careful quantification of charcoals found in numerous organic matter profiles per site) have allowed us to obtain a good estimation of initial stand conditions (depth of residual organic matter and initial tree composition). The tree composition and residual organic matter data showed a strong bimodal distribution (Appendix 2.A). Because of this, we classified all stands in one of two categories of stand composition (dominance by *P. banksiana* or *P. mariana*, based on the relative basal area of living and dead trees, and in one of two categories of fire severity (high severity fire = thin residual organic matter layer; low severity fire = thick residual organic matter layer). Because no stands that were dominated by *P. banksiana* showed a thick residual organic matter layer (= low severity fire), this classification resulted in three distinct chronosequences : *P. mariana* established after a low severity fire, *P. mariana* established after a high severity fire and *P. banksiana* established after a high severity fire.

According to the basal area of live and dead trees, 19 of the 48 sampled stands were dominated by *Pinus banksiana* after fire (Appendix 2.A). For the remaining 29 sites, as no significant traces of any other tree species except for *Picea mariana* were found among the deadwood or among macro-remains within forest floor profiles described

above (Appendix 2.A), these sites were all classified as being dominated by *P. mariana* after fire.

Sites were classified as originating either from a high severity (HS) or low severity (LS) fire based on the average thickness of the residual organic matter obtained from both the monoliths and the pits / trenches. A study of seven burns in the boreal forest has demonstrated that coniferous post-fire seed germination was significantly impacted when residual organic matter approached 5 cm (Greene, 2004). We used this ecologically significant threshold (4 cm) to classify soil burn severity. Among the stands sampled, 11 of the 29 *P. mariana* stands were established after the passage of a LS fire (Appendix 2.A).

2.4.3 Statistical Analyses

To obtain an integrated representation of the forest structure and to evaluate the factors responsible for the variation in forest structure, a canonical correspondence analysis (CCA) was computed using the program CANOCO Version 4 (Ter Braak & Šmilauer, 1999). The 'pseudo-species' variables used were the relative amount of stems in five height classes of live trees (2 – 4 m, 4 – 8 m, 8 – 12 m, 12 – 16 m, and > 16 m) and three dbh classes of dead trees (< 10 cm, 10 – 15 cm, and > 15 cm). The continuous environmental variables (mineral soil clay content, slope index and time since fire (TSF)), and categorical variables (fire severity and initial stand composition) were loaded by forward selection. Significance of each variable was computed using a Monte Carlo test ($\alpha = 0.05$).

We used regression analyses to assess the changes in forest structure with TSF and to test the effects of fire severity and initial composition. The following stand structural attributes were used: 1) basal area of live trees (height > 2 m), 2) basal area of large live trees (dbh > 10 cm), 3) density of saplings (height < 2 m), 4) basal area of large dead trees (dbh > 10 cm), 5) mean tree height (stems > 2 m), and 6) coefficient of variation of tree height (stems > 2 m). Since the CCA showed that slope index and soil texture were not significant in explaining stand structure, we have not included them in these analyses. As the chronosequences, based on initial composition and fire severity, spanned different time scales (*P. banksiana* high severity: 45 – 229 y, *P. mariana* low

severity: 38 – 169 y, and *P. mariana* high severity: 51 – 2355 y), we have analyzed the data at two distinct time scales: medium term (< 250 y) and long term (> 250 y). The medium term scale (< 250 y) was used to assess the effects of both fire severity and initial composition on stand structural development, while the long-term time scale (> 250 y) allowed us to evaluate how *P. mariana* stands established after high severity fires evolved in the extended absence of fire. Medium-term effects were assessed with a General Linear Model design (PROC GLM, SAS Institute, 2000) with a combination of a continuous predictor variable (TSF) and categorical predictor variables (initial stand composition and fire severity). When predictor variables or their interactions were non significant ($P > 0.05$) they were removed from the models. The quantitative effects of the extended absence of fire (> 250 yrs) on structural development were assessed with simple linear regression following appropriate transformation of the independent variable (TSF). The significance level ($\alpha = 0.05$) for both medium-term and long-term regressions was lowered to $\alpha = 0.025$ for the variables basal area of live trees and basal area of large live trees as these datasets were partly similar.

To assess if fire severity and initial composition influenced post-fire stand density and self-thinning, an analysis of variance was computed using only the younger stands (< 100 yrs). Since the two-way ANOVA design was incomplete (*i.e.*, no *P. banksiana* stands originating from a low severity fire), the specific effect of each independent variable was tested using planned comparisons. As previous work in the boreal forest has demonstrated that coniferous post-fire regeneration is limited to the first 5-10 y following fire (Gutsell & Johnson, 2002; Johnstone *et al.*, 2004), we estimated initial post-fire density as the total number of stems (live and dead) > 2 m in height, and the degree of self-thinning as the number of small dead stems (dbh < 10 cm). Among the 48 chronosequence stands, there were four pairs of young (< 100 y) *P. mariana* stands with each pair originating from the same fire but differing with respect to the severity of the last fire. These pairs were used to further test the effects of fire severity on initial stand densities and productivity using paired *t*-tests. For this comparison, three productivity variables were computed based on the mean height of the three, five or 10 tallest *P. mariana* stems.

2.5 Results

2.5.1 Ordination Trends

The canonical correspondence analysis showed that 1) the canonical axes 1 and 2 explained respectively 10% and 8% of the variance in stand structural characteristics (data not shown), and 2) fire severity explained 8% of the variation, time since fire 5%, and initial composition 4% (Table 2.1). The environmental variables, mineral soil clay content and the slope index did not significantly ($\square$ = 0.05) explain any more of the among-stand structural variability.

The ordination diagram showed that 1) fire severity was negatively correlated with axis 1 and positively correlated with axis 2, that 2) time since fire was positively correlated with both axes and that 3) initial stand composition was positively correlated with axis 2 (Figure 2.1A). The position of the pseudo-species centroids indicated that high proportions of large live stems (L4 and L5) and small dead stems (D1) were characteristic of stands established after high severity (HS) fires. Small live stems (L1, L2), positioned on the opposite side of the severity vector, were prevalent in stands originating from low severity (LS) fires. The position of large dead stems (D2 and D3) suggested that they were associated with old stands originating from HS fires and/or a post-fire dominance of *Pinus banksiana*. Finally, the position of intermediate live stems (L3) indicated that they were important in young stands regardless of fire severity.

The successional vectors, which connect the mean ordination score of each age-class from youngest to oldest for each chronosequence, revealed two major trends. First, the length of the HS fire vectors connecting the youngest age class (< 100 y) to the intermediate age class (100 - 200 y) suggested that the post-fire dominance of *P. banksiana,* while not affecting the direction of structural development, may have accelerated the rate of succession (compare solid and dashed vectors in Figure 2.1B). Second, while fire severity induced diverging short-term structural development pathways, the prolonged absence of fire brings about a convergence of *Picea mariana* stand structure regardless of fire severity (compare dashed and dotted vectors in Figure 2.1B).

2.5.2 Medium-Term Effects Of Stand Composition And Fire Severity

The presence of *Pinus banksiana* after HS fires did not affect post-fire stand densities (7600 vs. 9517 stems ha^{-1}; $P = 0.20$) or the degree of self-thinning as measured by the number of small dead stems (2329 vs. 3625 stems ha^{-1}; $P = 0.06$; data not shown otherwise). On the other hand, *Picea mariana* stands established after LS fires had significantly lower initial stand densities (6071 vs. 9517 stems ha^{-1}; $P = 0.03$) and experienced less self-thinning (328 vs. 3625 dead stems ha^{-1}; $P < 0.0001$; data not shown otherwise) than HS fires.

The post-fire dominance of *P. banksiana* had little effect on the evolution of forest structure (Table 2.2). After HS fires, stand basal area and mean stem height decreased as the variability in stem height increased with the continued absence of fire (Figure 2.2). Canopy closure, as measured by the amount of large live stems, peaked at 103 y to subsequently drop significantly (Figure 2.2B), while the density of saplings increased (Figure 2.2C). Since the basal area of large dead stems increased at a faster rate when *P. banksiana* dominated the initial composition (Figure 2.2D), the post-fire dominance of *P. banksiana* appeared to accelerate stand break up. In contrast, stands originating from LS fires initially showed low basal area of live trees and low mean tree height that both increased with time. Although LS fire stands showed lower basal area (Figures 2.2A & B), fire severity did not significantly affect stand break-up as measured by the amount of large dead stems (Table 2.2, Figure 2.2D). While fire severity had a significant short-term effect on forest structural development (Table 2.2, Figure 2.2), the different structural development pathways caused by fire severity converged after 150-200 y (Figure 2.2).

Stand height development after HS fires was characterized by a rapid establishment of a dense stand dominated by tall stems, which gradually evolved into an open stand dominated by short stems (Figure 2.3). There was no difference between the mean height structure of *P. banksiana* and *P. mariana* stands originating from HS fires (Kolmogorov-Smirnov two-sided test, □ = 0.05). In contrast, stands established after LS fires evolved from an initially open structure with few tall stems, to one that is relatively more closed, while still maintaining a high proportion of short stems. Stands established after LS fires thus showed in the first century after fire a height structure that was

significantly ($\alpha = 0.05$) different from that of stands established after HS fire; that difference was no longer visible in stands aged between 100 and 200 y old (Figure 2.3).

The comparison of the four paired *P. mariana* stands confirmed that LS fires resulted in lower initial tree densities as compared to high severity fires (Table 2.3). When the mean height of only the three tallest trees was considered, no difference in height was observed between severity types. However, as the number of trees increased, a difference in tree height emerged, mostly caused by a lower mean tree height in stands established after LS fires (Table 2.3). Although the use of multiple tests on mostly the same subset of trees hinders the strict interpretation of *P*-values, this trend suggests that the effects of fire severity on stand productivity are a result of both a lower post-fire recruitment and a subsequent higher variability in within-stand stem height growth after LS fires.

2.5.3 Extended Absence Of Fire And Stand Structural Development

The structural evolution of stands established after HS fires continued in the extended absence of fire (> 250 y) but at a much reduced rate (Figure 2.4). In comparison with the evolution observed during the first few centuries after fire (Figure 2.2), the changes occurring after 250 y appeared to be minimal (Figure 2.4). Interestingly, stand characteristics of old *P. mariana* stands established after HS fires resembled those of relatively young stands established after LS fires (Figure 2.4).

2.6 Discussion

2.6.1 Initial Composition

Initial post-fire tree composition had little influence on forest structural development. Although we hypothesized that the co-dominance of *Pinus banksiana* would affect within-stand stem height distribution, we observed no difference between the two composition types (Table 2.2, Figures 2.2 & 2.3). This may reflect the plasticity of *P. mariana* with respect to its ability to grow as an early successional fast-growing species and as a late successional shade-tolerant species (Dix & Swan, 1971). Similarly, there was no difference in post-fire density or stand basal area between stand composition

types (Figure 2.2, Table 2.2). This suggests that under similar post-fire abiotic conditions, *P. mariana* stands may be as productive as *P. banksiana* co-dominated stands.

While there appeared to be little difference in the timing of stand break-up between the two composition types (Figure 2.2B, Table 2.2), *P. banksiana* stands seemed to have broken up at a quicker rate than *P. mariana*-dominated stands (Figure 2.2D). This may have been due to the shorter longevity of *P. banksiana* or to species-specific pathogens like the Swaine jack pine sawfly (*Neodiprion swainei*) or the jack pine budworm (*Choristoneura pinus pinus*) (Martineau, 1984). Stand reconstruction studies could clarify the timing, rate, and causes of stand break-up in the coniferous boreal forest of the Clay Belt.

2.6.2 Fire Severity

Fire severity, defined as the thickness of the unburned soil organic matter, had a determinant influence on the structural development of the Clay Belt's forests. Most structural attributes evolved differently along the LS and HS fire chronosequences (TSF x fire severity interaction), and the large initial differences between severity types (HS vs. LS) eventually disappeared as the forest structure converged. This convergence may account for the small explanatory power of the CCA (Figure 2.1), that considered only primary effects. *Picea mariana*-dominated stands established after LS fires were less productive (lower stand basal area) than those established after HS fires. This loss in productivity appears to have been due to both a lower initial recruitment and a lower growth rate of trees. Our results corroborate other studies which have shown that recruitment of most coniferous boreal species is inversely related to the amount of organic matter remaining after fire (Chrosciewicz, 1976). It is hypothesized that residual duff, by altering seedbed physical and chemical properties, makes microsites less suitable for seed germination and/or seedling survival (Zasada *et al.*, 1983; Foster, 1985; Charron & Greene, 2002). However, since post-fire regeneration not only depends on seed bed suitability but also on the amount of seeds available for recolonization (Sirois & Payette, 1991; Payette *et al.*, 2000), we cannot rule out that differences in seed availability between severity types could have been an additional factor that contributed to reduce post-fire regeneration.

The comparison of same age stands from different fire severity types showed that site productivity was similar when only the three tallest trees were compared (a method commonly used in forest growth and yield inventories). A difference emerged however when additional trees were used, suggesting that a lower number of trees had optimal growing conditions in LS stands. This could be explained by the heterogeneity of post-fire seedbeds. High severity fires, by fully consuming the forest floor, bequeath to the next generation of trees a relatively homogeneous environment composed mostly of favorable microsites for seed germination and seedling growth. On the other hand, LS fires create a heterogeneous post-fire environment composed of few microsites favorable to seed germination and seedling growth, and a high frequency of poor microsites. This heterogeneity of microsites has a major influence on growth variation and size inequality in *P. mariana* stands (Macdonald & Yin, 1999). We postulate that the depressed productivity observed after LS fires is a consequence of the heterogeneity of microsites in these sites. Additionally, LS fires favor species that resprout after fire, notably competing shrubs such as *Ledum groenlandicum* and members of the Sphagnaceae (Dyrness & Norum, 1983; Purdon *et al.*, 2004), both of which are known to degrade growing conditions for trees (Heinselman 1963; Inderjit & Mallik, 1996). Of equal importance for understanding the reduced productivity associated with LS fires may be the openness of these stands, which increases the prevalence of frost events in late spring or early summer and may further hinder tree growth (Langvall & Örlander, 2001).

In the end, stand structural development during the first century after fire can de described as being affected by a series of positive feedback loops, which either favor or impede tree growth. Stand structure after HS fires is characterized by a high initial tree density that results in complete canopy closure, that in turn shades out competing vegetation and decreases the probability of growing-season frost events. On the other hand, stand structure after LS fires is characterized by a low initial tree regeneration and an abundant cover of shade-intolerant shrubs (*Kalmia*, *Ledum*) known to impede tree growth. The high cover of these competing species in LS fires (N. Lecomte, *pers. observ.)* might delay canopy closure and thus increase their own chance of survival and the prevalence of late spring / early summer frost events.

2.6.3 Convergence And Long-Term Stability Of The Closed Coniferous Boreal Forest

In the Clay Belt, a diversity of structural development pathways are present and the initial conditions (mostly fire severity) are important in determining the direction and rate of succession (Figure 2.5). Although fire severity induces diverging pathways of stand structural development in the short term, the prolonged absence of fire leads to a convergence of stand structure (Figure 2.5), as has been documented in other fire-dominated landscapes (Kashian, Turner & Romme, 2005; Kashian *et al.,* 2005). In the Clay Belt, the mechanisms driving this convergence of forest structure may be paludification, *i.e.*, the accumulation of soil organic matter, which is prevalent in the study area (Taylor, Carleton & Adams, 1987; Boudreault *et al.,* 2002). Paludification, by lowering soil temperatures and nutrient availability, significantly reduces stand productivity (Heinselman, 1963; Van Cleve & Viereck, 1981). Therefore in the prolonged absence of fire, all stands become paludified, averaging out post-fire differences in conditions caused by fire severity. This leads to a convergence in tree growth conditions and stand structural attributes regardless of initial tree composition or the severity of the last fire.

Previous studies have demonstrated that the fire cycle in the Clay Belt has been increasing since the end of the 'Little Ice Age' (*ca.* 1850) (Bergeron *et al.*, 2004b) and is predicted to continue to increase under current global climate change projections (Flannigan *et al.*, 2001). Given the structural development pathways described in this study (Figure 2.5), the continued decrease in fire frequency may have a detrimental effect on the long-term stability of the closed coniferous boreal forest. Long fire intervals may increase the probability of low post-fire densities because old stands with low basal area possibly produce fewer seeds (Black & Bliss, 1980; Sirois, 2000; Greene *et al.*, 2004), and accumulate excessive amounts of organic matter (Foster, 1985; Boudreault *et al.*, 2002) that are unlikely to be consumed completely by fire. Thus long fire cycles possibly reduce both the seed source and the post-fire availability of favorable seedbeds. In the end, if the fire regime becomes characterized by a lower fire frequency, the fires may also show reduced severity, which in the long run would reduce the proportion of dense productive stands in the landscape. Current provincial guidelines that *only* prescribe careful logging approaches that do not remove the soil organic layer (and are thus similar

to the effects of LS fires) may also give rise to a loss in stand productivity and stand structural diversity within this landscape especially among fine-textured deposits. In order to maintain both landscape stand productivity and stand diversity, future silvicultural approaches should concentrate on the removal of the soil organic matter to favor the establishment of dense productive stands similar to those established after HS fires. Our results suggest that the monitoring and manipulation of early seedling densities and microsite growth conditions should provide useful tools for the management of boreal stands in the Clay Belt.

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Table 2.1

Summary statistics of the canonical correspondence analysis (CCA) using the chronosequence dataset with a forward selection of environmental variables. Boldface *P*-values are significant at the 0.05 level.

Variable	% of variance explained	*F*	*P*
Fire severity	8	5.66	**0.005**
Time since fire	5	3.07	**0.015**
Initial tree composition	4	3.21	**0.02**
Mineral soil texture	2	1.09	0.32
Slope index	1	0.67	0.60

Table 2.2.

Results of the general linear models relating initial tree composition, fire severity, and time since fire to stand structural attributes using the medium term (< 250 y) chronosequence dataset (n = 42 stands).

Variable	Source	*F*	*P*
Basal area, live trees	Initial composition (COMP)	-	N.S.
$R^2 = 0.58$	Fire severity (SEV)	25.15	**<0.0001**
$P < 0.0001$	Time since fire (TSF)	2.81	0.1019
	COMP * TSF	-	N.S.
	SEV * TSF	7.67	**0.0086**
	TSF * TSF	-	N.S.
Basal area, large live trees	Initial composition (COMP)	-	N.S.
$R^2 = 0.54$	Fire severity (SEV)	30.89	**<0.0001**
$P < 0.0001$	Time since fire (TSF)	7.73	**0.0084**
	COMP * TSF	-	N.S.
	SEV * TSF	-	N.S.
	TSF * TSF	11.77	**0.0015**
Basal area, large dead trees	Initial composition (COMP)	0.74	0.3946
$R^2 = 0.51$	Fire severity (SEV)	-	N.S.
$P < 0.0001$	Time since fire (TSF)	72.83	**<0.0001**
	COMP * TSF	8.44	**0.0061**
	SEV * TSF	-	N.S.
	TSF * TSF	-	N.S.
Density, saplings	Initial composition (COMP)	-	N.S.
$R^2 = 0.28$	Fire severity (SEV)	9.18	**0.0044**
$P = 0.0058$	Time since fire (TSF)	0.34	0.5624
	COMP * TSF	-	N.S.
	SEV * TSF	6.09	**0.0182**
	TSF * TSF	-	N.S.
Mean tree height	Initial composition (COMP)	-	N.S.
$R^2 = 0.45$	Fire severity (SEV)	19.81	**<0.0001**
$P < 0.0001$	Time since fire (TSF)	0.39	0.5378
	COMP * TSF	-	N.S.
	SEV * TSF	8.89	**0.005**
	TSF * TSF	-	N.S.
CV mean tree height	Initial composition (COMP)	-	N.S.
$R^2 = 0.26$	Fire severity (SEV)	-	N.S.
$P = 0.0006$	Time since fire (TSF)	14.0	**0.006**
	COMP * TSF	-	N.S.
	SEV * TSF	-	N.S.
	TSF * TSF	-	N.S.

N.S. = non significant ($\alpha = 0.05$, except for Basal area, live trees and Basal area, large live trees, where the significance level was corrected ($\alpha = 0.025$) – see Methods).

Boldface *P*-values are significant at the 0.05 level.

Table 2.3.

Results of the paired *t*-tests for total density and mean height of four pairs of young (< 100 y) *Picea mariana* stands which originated after the same fire but differed with respect to the severity of the last fire.

Variable	High severity	Low severity	*P*
Total density (trees ha^{-1})	9825	7075	0.04
Mean height of 3 tallest trees (m)	13.42	11.7	0.11
Mean height of 5 tallest trees (m)	13.25	10.9	0.07
Mean height of 10 tallest trees (m)	13	9.93	0.03

Total density comprises all stems (live and dead) that were > 2 m in height

Appendix 2.A :
Characteristics of the chronosequence survey stands.

Site[1]	Initial Composition[2]	*Pinus banksiana* basal area[3] (m^{-2} ha^{-1})	Fire severity[4]	Residual OM[5] (cm)	Stand age (y)			Mineral soil			Slope index[9]
					Oldest tree[6]	Calibrated ^{14}C age (charcoal)[7]	Calibrated ^{14}C age (humus)[8]	Sand (%)	Silt (%)	Clay (%)	
30	Pine	29.5	High	1.2	45	-	-	1.5	22.0	76.5	1.0
54	Pine	43.6	High	1.0	51	-	-	0.0	12.7	87.3	1.9
61	Pine	32.5	High	1.5	51	-	-	6.5	21.5	72.0	5.1
36	Pine	39.4	High	1.6	76	-	-	1.0	23.6	75.4	0.6
38	Pine	23.1	High	1.6	84	-	-	0.0	9.0	91.0	0.7
23	Pine	32.0	High	1.3	86	-	-	3.5	26.9	69.7	1.4
57	Pine	34.2	High	1.2	88	-	-	13.0	45.5	41.5	1.2
29	Pine	39.9	High	1.2	135	-	-	19.9	30.8	49.3	1.2
69	Pine	34.2	High	1.1	139	-	-	2.0	34.3	63.7	1.9
66	Pine	28.5	High	1.7	149	-	-	12.5	25.0	62.5	8.7
73	Pine	50.8	High	1.3	149	-	-	26.0	25.0	49.0	1.5
40	Pine	35.6	High	1.1	151	-	-	25.5	27.5	47.0	2.4
49	Pine	28.4	High	1.2	155	-	-	14.0	63.0	23.0	2.1
94	Pine	44.7	High	1.0	176	-	-	6.0	24.5	69.5	5.1
83	Pine	40.0	High	1.0	177	-	-	4.0	20.0	76.0	1.0
79	Pine	20.1	High	1.1	179	-	-	2.4	29.0	68.6	0.0
65	Pine	32.8	High	2.1	204	-	-	14.0	32.5	53.5	0.8
64	Pine	25.8	High	1.9	222	-	-	0.0	38.4	61.6	3.9
67	Pine	15.2	High	1.0	229	-	-	0.0	28.6	71.4	1.4
62	Spruce	0.0	High	1.4	52	-	-	2.0	23.4	74.6	10.5
4	Spruce	0.0	High	2.5	53	-	-	0.0	38.1	61.9	2.5
59	Spruce	8.1	High	2.3	72	-	-	13.0	22.5	64.5	1.7
15	Spruce	2.4	High	1.5	76	-	-	10.3	27.9	61.8	-4.6
2	Spruce	0.0	High	1.9	84	-	-	0.0	21.0	79.0	0.6
56	Spruce	0.0	High	1.3	86	-	-	13.5	28.5	58.0	0.8
12	Spruce	0.4	High	1.1	94	-	-	0.0	20.9	79.1	2.1
55	Spruce	0.3	High	2.5	95	-	-	14.5	30.0	55.5	0.9
18	Spruce	0.0	High	2.0	126	-	-	15.0	18.0	67.0	1.8
75	Spruce	0.0	High	2.0	128	-	-	3.4	24.5	72.1	-1.3
8	Spruce	0.0	High	1.4	174	-	-	9.0	25.5	65.5	1.4
95	Spruce	0.0	High	1.3	184	-	-	3.0	26.0	71.0	1.7
9	Spruce	0.0	High	1.5	215	1225	-	11.5	23.5	65.0	1.6
7	Spruce	0.0	High	1.7	217	790	-	7.5	27.0	65.5	1.1
50	Spruce	0.0	High	2.0	222	365	-	19.0	27.0	54.0	1.3
6	Spruce	0.0	High	3.2	280	710	555	1.0	22.7	76.4	0.4
16	Spruce	0.0	High	2.7	286	1585	705	10.0	18.0	72.0	0.5
20	Spruce	0.0	High	3.2	353	2355	-	5.9	22.8	71.3	1.9
11	Spruce	0.0	Low	12.0	38	-	-	21.0	29.5	49.5	1.1
74	Spruce	0.0	Low	13.0	52	-	-	6.0	26.5	67.5	1.3
53	Spruce	0.0	Low	7.3	53	-	-	20.0	31.0	49.0	0.6
58	Spruce	0.0	Low	5.8	62	-	-	23.0	30.5	46.5	2.1
78	Spruce	0.0	Low	17.9	75	-	-	17.0	28.0	55.0	0.6
60	Spruce	0.0	Low	6.7	84	-	-	9.0	15.0	76.0	1.2
3	Spruce	0.0	Low	16.2	94	-	-	1.9	16.0	82.0	0.0
68	Spruce	1.6	Low	4.6	139	-	-	1.0	22.7	76.4	0.8
63	Spruce	0.0	Low	7.9	143	-	-	2.0	18.5	79.5	0.8
17	Spruce	0.0	Low	17.3	151	-	-	17.5	33.0	49.5	0.8
5	Spruce	0.7	Low	8.4	169	-	-	13.9	47.6	38.5	0.3

[1] Sites in boldface are the paired sites originating from the same fire but differing with respect to fire severity.
[2] Initial stand composition determined from the composition of dead and live trees (see Methods).
[3] Total amount of live and dead *P. banksiana* stems > 2 m in height.
[4] Fire severity determined from the thickness of the residual organic matter (see Methods).
[5] Thickness of the residual organic matter, *i.e.*, the organic matter that was not burned by the last fire, located between the mineral horizon and the uppermost charcoal layer.
[6] Stand age determined from tree-ring analysis. Stands where the postfire cohort of trees was not found were given a minimum age and were radiocarbon dated.
[7] Radiocarbon dates obtained for carbonized plant remains (see Methods).
[8] Radiocarbon dates obtained for humus accumulated just above uppermost charcoal layer (from Cyr *et al.*, 2005).
[9] Slope index integrates slope incline and landform shape, and can assume positive (mounds or regular slopes) and negative values (depressions) (see Methods).

2.8 Figure captions

Figure 2.1. Canonical correspondence analysis of stand structure (relative abundance of stems represented by eight pseudo-species based on status and stem size classes) using the chronosequence dataset. A) Pseudo-species (closed circles) and environmental variables (open squares for categorical variables, vector for the continuous variable). B) Successionnal vectors connecting the mean value of each age-class (< 100 y, 100-200 y, and > 200 y), from the youngest to the oldest, in the three chronosequences (PBA, Pinus banksiana; PMA, Picea mariana; HS, high severity fire; LS, low severity fire). Pseudo-species codes for live stems are L1 (height 2 - 4 m), L2 (4 - 8 m), L3 (8 - 12 m), L4 (12 - 16 m) and L5 (> 16 m), and for dead stems, D1 (dbh < 10 cm), D2 (10 – 15 cm), and D3 (> 15 cm). Environmental variables are as follows: TSF, time since last fire; SEV, centroid of stands originating from a high severity fire; COMP, centroid of Pinus banksiana-dominated stands.

Figure 2.2. Evolution of stand structural attributes with time since the last fire at a medium term time scale (< 250 y). Coefficients of determination and probability levels are in Table 2.2.

Figure 2.3. Height structure of stands (lines) in *Pinus banksiana* (PBA)-dominated stands originating from high severity (HS) fires (upper row), *Picea mariana* (PMA)-dominated stands originating from high severity fires (middle row), and *P. mariana* stands established after low severity (LS) fires (bottom row). The left column of graphs represent stands younger than 100 y, the middle column, stands aged between 100 and 200 y, and on the right, stands older than 200 y. Each line represents a stand. Height classes: 2 = 2-4 m, 4 = 4-8 m, 8 = 8-12 m, 12 = 12-16 m, 16 = > 16 m. Number of stands is indicated. Groups of stands showing a different letter within the same column have a significantly ($\alpha = 0.05$) different mean frequency distribution (two-sided Kolmogorov-Smirnov test).

Figure 2.4. Long-term evolution (> 250 y) of stand structural attributes in *Picea mariana*-dominated stands established after high severity fires.

Figure 2.5. Conceptualized development pathways of stand structure in the Clay Belt of northwestern Quebec. Stand structural diversity in this landscape is a function of the severity of the last fire (vertical vector) and the time elapsed since the last fire (horizontal vector). After high severity fires, the composition of the dense initial stands can vary between a complete dominance of *Picea mariana* to a co-dominance with *Pinus banksiana*. Eventually, all stands converge towards an open structured *P. mariana*-dominated stand after *ca.* 200 y.

Figure 2.1

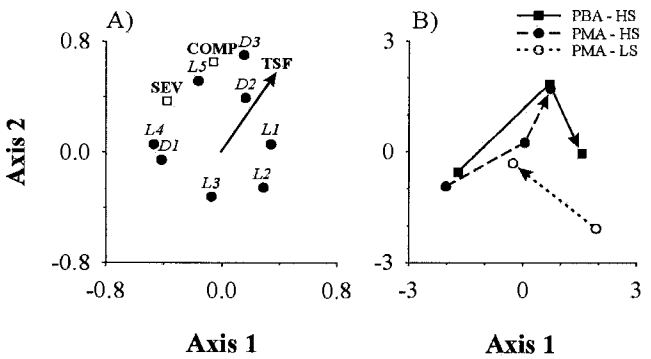
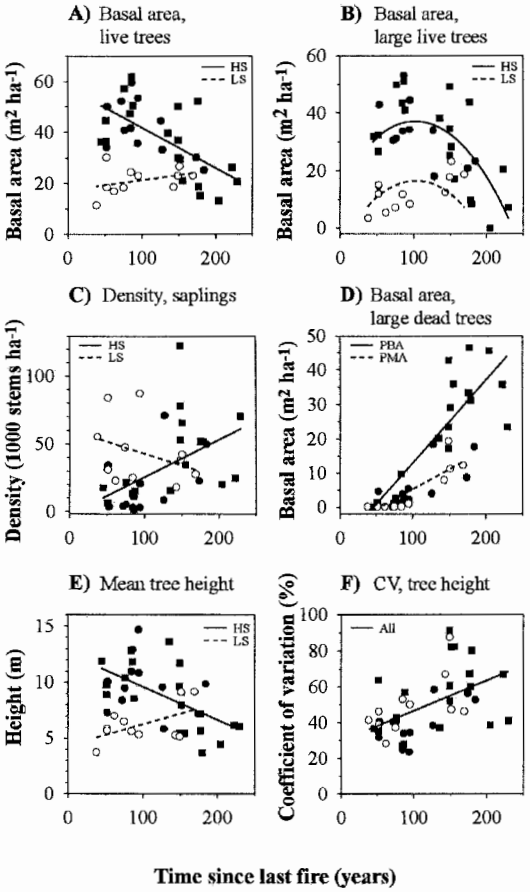

A)
B)
PBA - HS
PMA - HS
PMA - LS
COMP
D3
L5
TSF
SEV
D2
L4
D1
L1
L3
L2
0.8
0.0
-0.8
3
0
-3
Axis 2
Axis 1
Axis 1

Figure 2.2



- *Pinus banksiana* (PBA), high severity fires (HS)
- *Picea mariana* (PMA), high severity fires (HS)
- *Picea mariana* (PMA), low severity fires (LS)

Figure 2.3

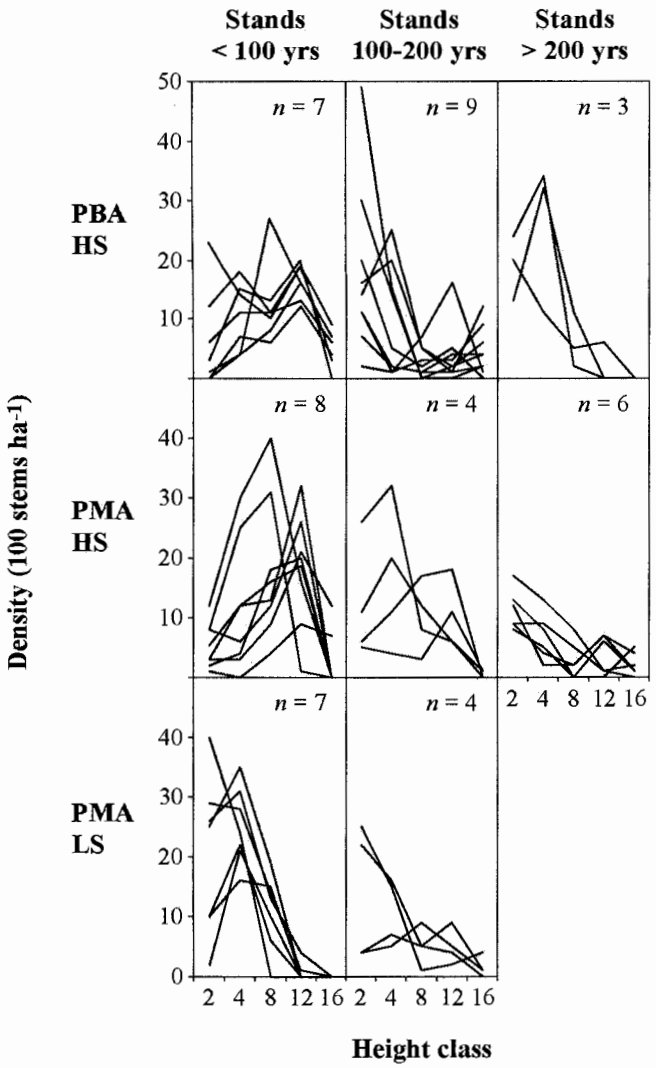

Stands
< 100 yrs
Stands
100-200 yrs
Stands
> 200 yrs
PBA
HS
PMA
HS
PMA
LS
n = 7
n = 9
n = 3
n = 8
n = 4
n = 6
n = 7
n = 4
Density (100 stems ha-1)
Height class
0
10
20
30
40
50
2 4 8 12 16

Figure 2.4

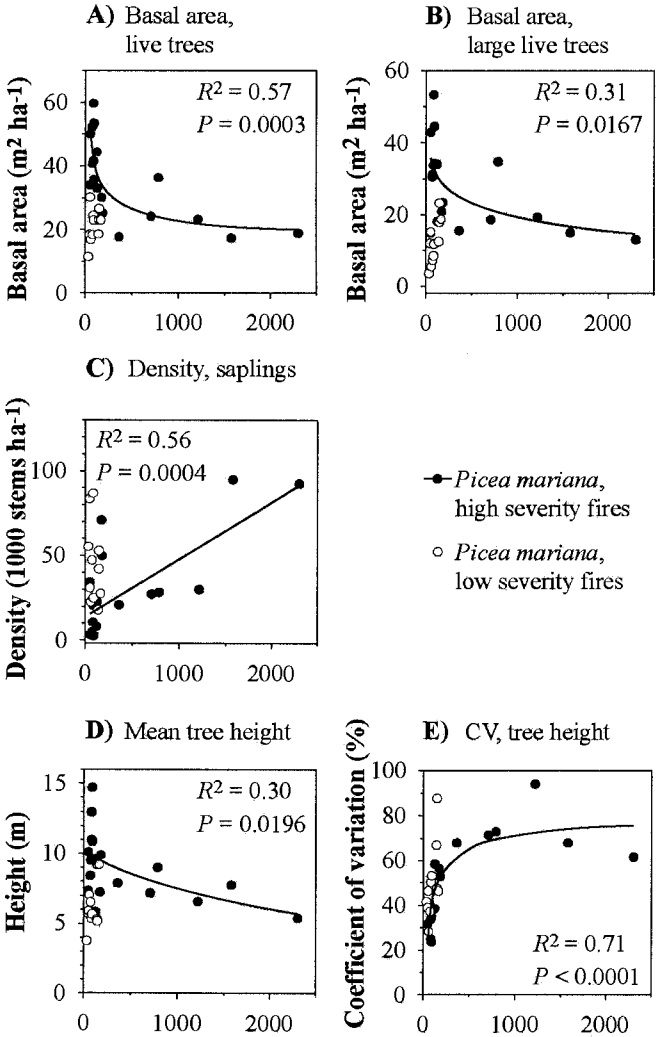
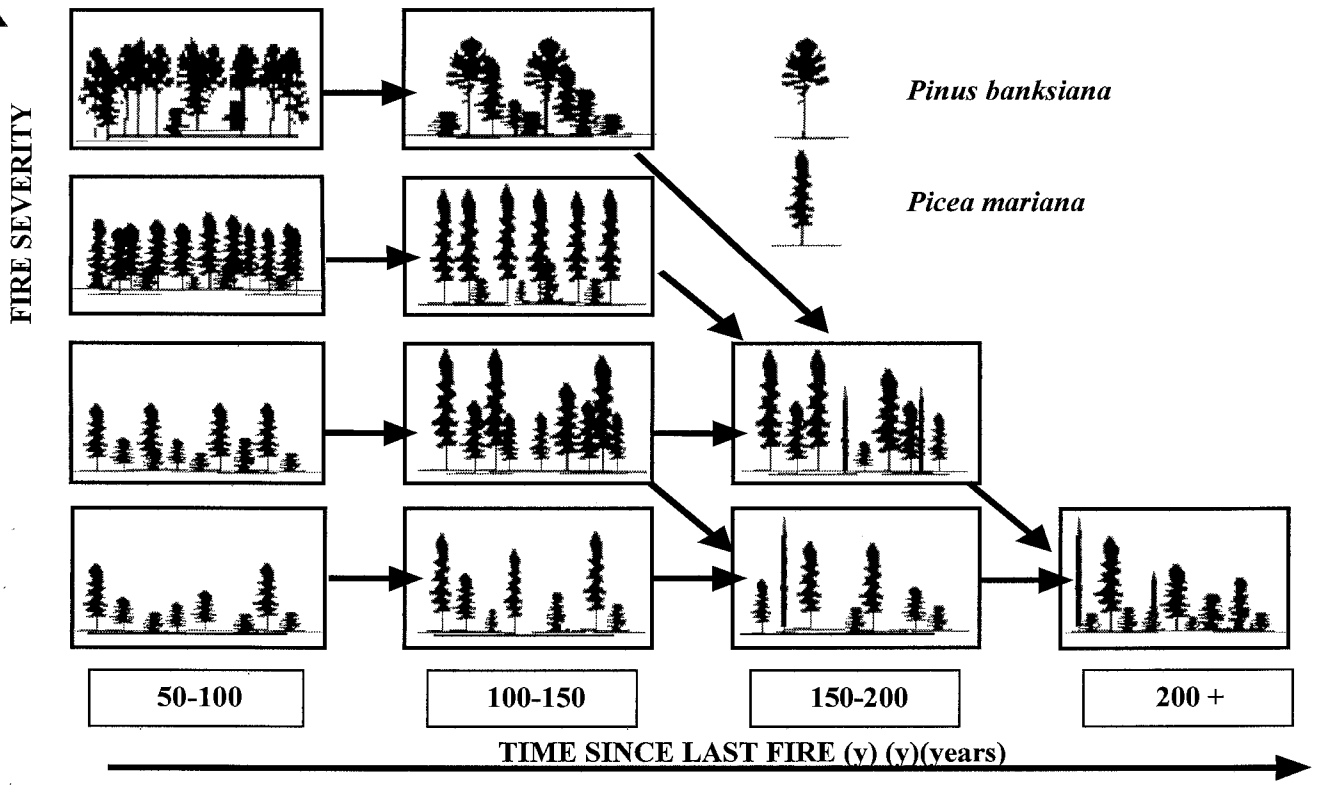

A) Basal area, live trees
B) Basal area, large live trees
C) Density, saplings
D) Mean tree height
E) CV, tree height
Basal area (m2 ha-1)
Density (1000 stems ha-1)
Height (m)
Coefficient of variation (%)
R2 = 0.57
P = 0.0003
R2 = 0.31
P = 0.0167
R2 = 0.56
P = 0.0004
R2 = 0.30
P = 0.0196
R2 = 0.71
P < 0.0001
Picea mariana, high severity fires
Picea mariana, low severity fires
Time since last fire (years)

Figure 2.5


FIRE SEVERITY
Pinus banksiana
Picea mariana
50-100
100-150
150-200
200 +
TIME SINCE LAST FIRE (y) (y)(years)

CHAPITRE III

Fire severity effects on ecosystem biomass dynamics in coniferous boreal forests of eastern Canada.

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Manuscrit soumis à *Ecosystems*

3.1 Abstract

The objective of this study was to characterize the effects of soil burn severity and initial tree composition on long-term forest floor dynamics and ecosystem biomass partitioning within the *Picea mariana* [Mill.] BSP-feathermoss bioclimatic domain of northwestern Quebec. Changes in forest floor organic matter and ecosystem biomass partitioning were evaluated along a 2355-yr chronosequence of extant stands. Paleoecological methods were used to determine the soil burn severity of the last fire (high vs. low severity) and the post-fire tree composition of each stand (*Picea mariana* vs. *Pinus banksiana* Lamb.). In stands originating from high severity fires, the post-fire dominance by *P. banksiana* had little effect on forest floor thickness or tree biomass productivity as compared to *P. mariana*-dominated stands. In contrast, stands established after low severity fires accumulated during the first century after fire nearly 50% thicker forest floors and produced 50% less tree biomass than stands established after high severity fires. Standing tree biomass increased until *ca* 100 yrs after high severity fires, and then decreased at a logarithmic rate in the millennial absence of fire. Forest floor thickness also showed a rapid initial accumulation rate, but continued to increase in the millennial absence of fire at a much slower rate. However, as forest floor density increased through time, the rate of increase in forest floor biomass (58 g m^{-2} yr^{-1}) remained constant for numerous centuries after fire (700 years). Whereas young stands (< 200 yrs) have more than 60% of ecosystem biomass locked-up in living biomass, older stands (> 200 yrs) sequester the majority (> 80%) of it in their forest floors. The results from this study illustrate that, under similar edaphic conditions, a single gradient related to time since disturbance is insufficient to account for the full spectrum of ecosystem biomass dynamics occurring in eastern boreal forests and highlights the importance of considering soil burn severity. Although fire severity induces diverging ecosystem biomass dynamics in the short term, the extended absence of fire brings about a convergence in terms of ecosystem biomass accumulation and partitioning.

Key words: Fire disturbance, forest succession, soil burn severity, forest floor organic matter, biomass partitioning, biomass accumulation, ecological convergence, chronosequence, black spruce (*Picea mariana*), jack pine (*Pinus banksiana*)

3.2 Résumé

L'objectif de l'étude était de caractériser les effets à long terme de la sévérité du feu et de la composition initiale sur la dynamique de la matière organique accumulée au sol et sur la distribution de la biomasse au sein du domaine de la pessière de l'Ouest du nord-ouest du Québec. Les changements dans la matière organique accumulée au sol et la distribution de biomasse ont été évalués le long d'une chronoséquence de 2355 ans. Des méthodes paléoécologiques ont été utilisées pour déterminer la sévérité du dernier feu et la composition après feu de chaque peuplement. La dominance après feu par *Pinus banksiana* a eu peu d'effet sur la matière organique ou la productivité de biomasse par les arbres. Pendant le premier siècle après feu, les peuplements établis après des feux peu sévères ont accumulé des couches de matière organique 50% plus épaisses, mais aussi 50% moins de biomasse d'arbres que les peuplements établis après des feux sévères. Après des feux sévères, la biomasse vivante d'arbres augmenta jusqu'à *ca* 100 ans, et diminuera ensuite avec un taux logarithmique en l'absence millénniale du feu. L'épaisseur de matière organique démontra également une augmentation initiale rapide qui continua dans l'absence millénniale du feu mais à un taux beaucoup plus lent. Toutefois, puisque la densité de la matière organique augmenta pendant uneabsence millénniale du feu, le taux d'accumulation de biomasse augmenta avec un taux linéaire (58 g m^{-2} yr^{-1}) qui demeura constant pendant plusieurs siècles après feu (700 ans). Quoique les jeunes peuplements (< 200 ans) avaient plus que 60% de la biomasse de l'écosystème comprise dans la partie vivante du peuplement, en absence prolongée de feu (> 200 ans), la majorité (> 80%) se retrouve dans la matière organique accumulée au sol. Les résultats de l'étude illustrent que sous des conditions édaphiques similaires, un gradient relié au temps depuis la dernière perturbation est insuffisant pour expliquer toute la gamme de processus associés à l'accumulation et à la distribution de matière organique dans les forêts boréales de l'Est. Ils illustrent aussi l'importance de considérer la sévérité du feu.

3.3 Introduction

Boreal forests play an important role in the global carbon cycle hence many studies have tried to understand how global climate change may affect boreal forest dynamics (e.g. Kasischke and others 1995; Kurz and Apps 1999). In boreal forest ecosystems, carbon is stored in two main pools: living tree biomass and the forest floor organic matter accumulated above the mineral soil (Gower and others 1997; O'Connell and others 2003; Wang and others 2003). The accumulation of organic carbon and the distribution of this carbon among these pools is however not homogeneous among and within boreal landscapes (Gower and others 1997; 2001; Yu and others 2002; Bhatti and others 2002; Swanson and others 2000). Understanding the factors responsible for this variability is of critical importance if we are to properly estimate the role of boreal forests in current and future global carbon cycling.

In the boreal forest, fire is the main disturbance that terminates / initiates secondary succession and redistributes biomass between the forest floor and living trees (O'Neill and others 2004; Wardle and others 1997; 2003). Relatively short fire cycles (< 100 years) predominate in the western and central portions of the North-American boreal biome (Johnson 1992). However studies in the eastern portion of this biome, which is under the influence of a humid maritime climate, have documented much longer current fire cycles (> 300 yrs; Foster 1983; Bergeron and others 2004a; Cyr and others 2005). Longer fire cycles may engender a prevalence of low severity fires that do not fully consume the thick and dense forest floor organic matter that accumulates during long fire-free periods (Foster 1985; Simon and Schwab 2005). To date, most biomass accumulation studies have been undertaken in the western and central portions of the boreal forest and as a result researchers have concentrated their efforts on the effects of high severity fires at relatively short time scales (0-150 years) (e.g. Kurtz and Apps 1999; Wang and others 2003; Gower and others 1997). Because old stands (> 150 years) and low severity fires can predominate in some eastern boreal landscapes (Foster 1985; Simon and Schwab 2005; Bergeron and others 2004b), to properly estimate the role of eastern boreal forests in the global carbon cycle, we need to understand how fire severity influences biomass sequestration as succession proceeds in the extended absence of fire (> 150 years).

Fire cycles vary spatially (e.g. Amiro and others 2001) and temporally (Bergeron and others 2001) across the boreal zone and changes in fire frequency may result in changes in the frequency of successional pathways co-occurring under similar edaphic conditions (e.g. Johnstone and Chapin 2005; LeGoff and Sirois 2004; Parisien and Sirois 2003; Larocque and others 2000). Within eastern boreal landscapes, short fire intervals favor species that reach sexual maturity quickly such as *Pinus banksiana* Lamb. to the detriment of slower-maturing species such as *Picea mariana* [Mill.] BSP. On the other hand, long fire intervals will tend to favor longer-lived species or species that are able to regenerate in the absence of fire such as *P. mariana* and unlike *P. banksiana.* Given that *P. banksiana* is a fast-growing early successional species and that it produces higher quality litter (higher C : N ratio) than *P. mariana* (Preston and others 2002), initial tree composition may influence ecosystem biomass accumulation and partitioning. As global climate change will certainly influence fire frequency (Kasischke and others 2001; Flannigan and others 2001), understanding how global climate change may influence biomass sequestration in the eastern boreal necessitates an understanding on how biomass sequestration differs along multiple successional pathways co-occurring under similar edaphic conditions.

In this paper, we report on the effects of the initial tree composition and fire severity on long-term forest floor dynamics and ecosystem biomass partitioning in coniferous stands on fine-textured deposits. We refer to fire severity exclusively as the effects of fire on the accumulated soil organic matter (quantity of duff burned / unburned *sensu* Miyanishi and Johnson 2002) as opposed to the effects of fire on the canopy (% trees killed; *sensu* Greene and others 2004). We hypothesized that among-stand diversity in forest floor thickness and biomass partitioning can be explained by the initial post-fire stand conditions and by processes operating in the absence of fire at the stand scale. Given that short-term studies indicate that fire severity affects seed germination (Chrosciewicz 1974; 1976; Zasada and others 1983), subsequent tree growth (Zasada and others 1987) and soil temperature and nutrient availability (Van Cleve and Viereck 1981; Van Cleve and Dyrness 1983), we hypothesize that low severity fires will depress tree biomass production and result in altered biomass partitioning as compared to high severity fires. Due to the higher quality litter and faster growth of *P. banksiana* as compared to *P. mariana*, we hypothesize that the post-fire stand dominance by *P.*

banksiana may increase decomposition rates and consequently reduce forest floor thickness and increase the amount of biomass accumulated in living trees.

3.4 Methods

3.4.1 Study area

The study area is part of the Lake Matagami Lowland ecological region, within the *Picea mariana*—feathermoss bioclimatic domain (Saucier and others 1998). This area is located within the Clay Belt of northeastern Ontario and northwestern Quebec, a physiographic unit composed primarily of clay deposits left by pro-glacial Lake Ojibway (Veillette 1994). Although a few rocky outcrops are scattered across the landscape, the topography is generally flat. Average annual temperature (1971-2000) recorded at the closest weather station to the North (Matagami, 49° 46'N, 77° 49'W) and to the south (La Sarre, 48° 46'N, 79° 13'W) are respectively –0.7 ° C and 0.7 ° C with an average of 906 mm and 890 mm of precipitation annually (Environment Canada, 2005). While agricultural settlement south of the study area began in the middle of the 1930s, intensive logging of this area only began in the late 1970s. Most of the area is covered by structurally diverse coniferous forests dominated either by *Picea mariana* or *Pinus banksiana* (Harper and others 2002) with a forest floor dominated either by *Sphagnum spp.* or *Pleurozium schreberi* (Boudreault and others 2002). Occasional deciduous stands (*Populus tremuloides* Michx. and *Betula papyrifera* Marsh.) are dispersed across the landscape. Fire is the main disturbance that terminates and initiates secondary successions. Fire cycle length has increased from 101 years before 1850, to 135 yrs between 1850 and 1920, to 398 yrs since 1920; mean stand age is 148 years (Bergeron and others 2004b). Compared to regions further east and south, the spruce budworm, *Choristoneura fumiferana* (Clem.), has a markedly reduced impact in this area. Both historical patterns of budworm defoliation (Boulet et al. 1996; Gray et al. 2000) and tree-ring reconstructions (M. Simard, N. Lecomte, and Y. Bergeron, *unpublished data*) show that spruce budworm has a negligible impact in these black spruce-dominated forests.

3.4.2 Data sets

To investigate the role of fire severity and initial composition on forest floor organic matter accumulation and ecosystem biomass partitioning, three data sets were used. The first data set (214 stands) is a compilation of forest inventory plots measured by the Quebec Ministry of Natural Resources (QMNR) in 1996. The second data set (48 stands) represents a chronosequence survey that was undertaken between 2000 and 2003, and is representative of stands from the landscape survey with a bias towards coniferous stands on fine-textured deposits. The final data set (8 stands) is a survey of forest floor organic matter that was undertaken in 2003 among a representative subset of *P. mariana* stands from the chronosequence survey.

3.4.3 QMNR landscape survey

Since the QMNR inventories the forest for forestry purposes, forest stands on slopes > 40% and with a canopy shorter than 7 m were not sampled. In the study area, 214 circular plots of 400 m^2 were sampled. In each plot, every tree with a diameter at breast height (dbh) > 10 cm was identified to species and tabulated in 2-cm diameter classes, while trees with dbh < 10 cm were sampled in a concentric subplot of 40 m^2. In each plot, the age at breast height of three dominant stems was determined from increment cores. Slope quantification, mineral soil classification and the measurement of the thickness of the forest floor (L, F and H horizons) were done on site (Saucier 1994). By overlaying fire reconstruction maps (Bergeron and others 2004b) onto the forest inventory, a date since last fire was assigned to every forest stand, and was further validated using the oldest age determined for the three dominant trees per stand. The fire reconstruction maps were developed by dating fire scars and post-fire tree cohorts, and by using archives and aerial photographs for recent fires (see Bergeron and others 2004b for further details).

3.4.4 Chronosequence survey

3.4.4.1 Site selection and tree sampling

Within the area covered by the QMNR survey, we visited all the burned areas that were located < 2 km from a road. In all, 43 distinct fires of different age were sampled. In each

fire, the density and composition (*P. mariana* vs. *P. banksiana*) of the post-fire tree cohort was estimated based on current and/or deadwood tree composition. When different post-fire densities and compositions were observed within the same fire, several stands were sampled. Each stand had to be on fine-textured mineral deposits, on a slight incline and free of any sign of anthropogenic disturbance. In a 10 m x 10 m representative quadrat, the height and dbh of all live and dead stems > 2 m in height were measured for each tree species. Dead trees buried under the organic matter were exhumed, measured and identified to species based on bark, branching and wood morphology. Origin of dead stems (pre or post-fire) was assessed with the presence / absence of charcoal.

3.4.4.2 Soil Analyses and Topography

Although the mineral soil texture was hand-checked *in situ*, to insure that all sites were comparable with respect to soil texture, mineral soil samples were taken at the center of each quadrat, one at the surface and another at a depth of 1m. The samples were air dried, analyzed for texture (Bouyoucos hydrometer method (McKeague, 1976)) and then the results from the two horizons were averaged to obtain the percentage of sand, silt and clay of the mineral soil per site.

While in general the Clay Belt's topography may be considered flat, peat accumulation may mask the original mineral soil topography. A theodolite was therefore used to characterize the topography of the area surrounding each stand by noting the relative heights of points positioned every 10 m along four 50 m transects each starting at the center of the quadrat and passing through one of the 4 corners. For each transect, we calculated the slope of the mineral soil. Transects with slopes which were not significant ($p > 0.05$) were given a value of 0. If the slopes of transects going in opposite directions were of opposite signs or if one or both of the slopes was null, we calculated the slope of the two transects combined (i.e., one transect of 100 m). If the slopes were of the same sign, we summed these slopes to obtain a negative slope value (depression) and positive value (mound or incline) for the 100 m transect. The Slope Index used in this study is the mean of the slopes of the two 100 m transects.

3.4.4.3Stand age determination

Stand age (fire year) for the youngest stands (< 100 years old) was determined from a stand initiation map (Bergeron and others 2004a) and was validated by counting rings from cross-sections taken at the base of dominant trees. In older stands, stand age was obtained by carefully dating cross-sections taken at the base of live and dead dominant trees. Cross-sections were finely sanded and crossdated using a frost-ring chronology under a dissecting microscope at 40x magnification. Crossdating was verified using the program COFECHA (Holmes 1983). In stands where the oldest tree was more than 200 years of age, and no fire scars or pioneer species (*P. banksiana*) were found, samples of carbonized plant remains from the uppermost charcoal layer of the forest floor were sent to IsoTrace Laboratories (Toronto, Canada) for AMS (Accelerator Mass Spectrometry) radiocarbon dating. The radiocarbon years were calibrated in calendar years using INTCAL98 (Stuiver and others 1998) (Appendix 3.A). Radiocarbon datings from a parallel study (Cyr and others 2005) undertaken in two of the older stands (> 250 years) are also shown (Appendix 3.A). In this study however the authors dated the organic matter located just above the uppermost charcoal layer within the forest floor profile. This may account for the younger dates this study obtained as compared to our radiocarbon dates from carbonized material. Nonetheless, as the radiocarbon dates of humus predate the age of the oldest tree present, we used the dates obtained from carbonized plant remains.

3.4.4.4 Fire Severity

At each stand, the severity of the last fire was qualified based on the average thickness of duff that was not consumed by the last fire, i.e., the residual organic matter (ROM). Ideally soil burn severity is quantified as the amount of organic matter consumed (*sensu* Myanishi and Johnson 2002). Nonetheless, as it is impossible to know how much organic matter was present in the pre-fire stand, we have chosen to qualify fire severity as the amount of organic matter not consumed by the fire (e.g. Xuan-Nguyen and others 2000). The thickness of the ROM was measured with two methods: by meticulous laboratory analysis of a few forest floor profiles per site, and by careful *in situ* observations of charcoal layers within numerous pits and trenches dug into the forest floor. At each site, between 2 and 4, 10 cm x 10 cm monoliths of the organic layer were

cut down to the mineral soil with a Wardenaar sampler. The monoliths were frozen and then sliced into 1-cm sections. Subsamples of 50 cm^3 were defloculated in a 2% NaOH solution for 24 h at 60 °C before a gentle manual water spray was used to sieve the samples through a 2 mm mesh. Samples were then bleached in a 10-20% HCl solution and observed microscopically at 40x magnification. Individual plant remains were identified by type (cone scales, leaf fragments, seeds, etc.) and to species, genus or family depending on extent of decomposition. The relative abundance of each plant remain type was then quantified (0-12.5%, 12.5-25%, 25-50%, 50-75%, 75-100%). Charcoal fragments were extracted, dried and then weighed The mineral soil / organic matter interface of each monolith was established where the mineral soil represented less than 25% of the particles retained in the 2 mm mesh. The thickness of the residual organic matter was calculated as the number of layers above the mineral soil but under the last layer deposited to contain more than 0.001 g of charcoal.

In the younger black spruce sites (< 200 yrs), 2.25-m trenches were dug about 20 cm into the mineral soil. At every 15 cm along the trench, the depth of the uppermost charcoal layer and of the mineral soil were noted, so that the thickness of the residual organic matter and of the organic matter accumulated since the last fire (Post-fire forest floor thickness) could be calculated as well as the total thickness of the forest floor (L, F, and H horizons; Post-fire forest floor thickness and ROM thickness combined). Additionally, in each *P. banksiana* and *P. mariana* stand, respectively ten and fifteen 25 x 25 cm pits were dug into the mineral soil every 2 m along two or three 10-m transects. For each pit, the same measurements were noted as done for the trenches.

3.4.4.5 Site classification

The substitution of time by space (chronosequence approach) to understand long-term stand dynamics has been widely used but also extensively criticized. The main potential drawback of using a chronosequence approach is the possibility of selecting stands that differ with respect to their biophysical site characteristics and/or initial conditions after the stand-replacing disturbance. We carefully selected and characterized the biophysical conditions of stands to reduce variability in surficial deposit and slope (Appendix 3.A, Table 3.1). Furthermore, we are confident that the paleological methods used in this study (exhumation and identification of dead wood, careful quantification of

plant macroremains and charcoals found in numerous organic matter profiles per site) have permitted us to obtain a good estimation of initial stand conditions (depth of residual organic matter and initial tree composition). The tree composition and residual organic matter data showed a strong bimodal distribution (Fig 3.1a, 3.1b). Because of this, we classified all stands in one of two categories of stand composition (dominance by *P. banksiana* or *P. mariana*, based on the relative basal area of living and dead trees), and in one of two categories of fire severity (high severity fire = thin residual organic matter layer; low severity fire = thick residual organic matter layer). Because no stands that were dominated by *P. banksiana* showed a thick residual organic matter layer (= low severity fire), this classification resulted in three distinct chronosequences : *P. mariana* established after a low severity fire, *P. mariana* established after a high severity fire and *P. banksiana* established after a high severity fire.

According to the basal area of live and dead trees, 19 of the 48 sampled stands were dominated by *Pinus banksiana* after fire (Fig 3.1a). For the remaining 29 sites, as no significant traces of any other tree species except for *Picea mariana* were found among the deadwood or among macro-remains within forest floor profiles described above (Appendix 3.A), these sites were all classified as being dominated by *P. mariana* after fire.

Sites were classified as either originating from a high severity (HS) or low severity (LS) fire based on the average thickness of the residual organic matter obtained from both the monoliths and the pits / trenches. A study of seven burns in the boreal forest has demonstrated that coniferous post-fire seed germination was significantly impacted when residual organic matter approached 5 cm (Greene 2004). We used this ecologically significant threshold (5 cm) to classify soil burn severity. Among the stands sampled, 11 of the 29 *P. mariana* stands were established after the passage of a LS fire (Fig. 3.1b).

3.4.5 Forest floor survey

To quantify forest floor biomass accumulation, a subset of 8 HS fire stands were selected among the 29 black spruce-dominated stands. The stands were chosen according to their accessibility and age, so that they still represented a chronosequence spanning numerous decades (> 700 years). At each site, 5 pits were dug at 4-m intervals along a

randomly placed 20-m transect. In each pit, a 10 cm x 10 cm x 5 cm sample of organic matter was retrieved at a depth of 10 cm below the surface (Upper forest floor Organic Matter) and another immediately above the charcoal layer of the last fire (Lower forest floor Organic Matter). When total forest floor thickness was less than 15 cm thick, only one sample was taken and identified as the Upper forest floor Organic Matter. Each sample was delicately cut out from the pits and brought back to laboratory in rigid containers to avoid altering its volume. We removed roots from a subsample, which was trimmed to fit inside an open container of known volume, then dried and weighted to calculate its density. Organic matter density for each site was calculated by first averaging the density of the Upper and Lower horizons for each pit, and then by calculating the mean density of the five pits. The mean organic matter density data per site were then coupled to the forest floor thickness data to calculate forest floor organic matter biomass per site on an areal basis.

3.4.6 Statistical analyses

3.4.6.1 QMNR data set

Given the fact that *P. mariana* replaces *P. banksiana* when the fire interval exceeds 100 years (Harper and others 2002) and that we have no information on the composition of deadwood in the stands sampled by the QMNR, we only used stands < 100 year-old from this data set (102 stands). We checked for differences in slope and stand age, and compared the forest floor thickness and stand basal area of the two composition types using a *t*-test, or a modified *t*-test when their variance was not equal. Fire severity was not tested with this dataset as the QMNR does not qualify the severity of the last fire during its inventory. The response variables that were investigated are stand basal area and total forest floor thickness. The independent variable was Stand Composition (categorical variable: *Picea mariana*- and *Pinus banksiana*-dominated stands).

3.4.6.2 Chronosequence data set

The chronosequence database, that spanned different time scales depending on fire severity and initial composition (*P. banksiana* HS fires: 45 – 229 years, *P. mariana* LS fires: 38 – 169 years, and *P. mariana* HS fires: 52 – 2355 years), was analyzed at two

distinct time scales: medium term (< 250 years) and long term (> 250 years). The medium-term scale (< 250 years), allowed us to assess the effects of both fire severity and initial composition on ecosystem biomass dynamics, and to compare these results to those obtained with the QMNR data set. The long-term scale (250 - 2500 years) allowed us to evaluate how *P. mariana* stands established after HS fires evolved in the extended absence of fire.

Topography (Slope Index) and soil variables (percent sand, silt, and clay) were not used in the chronosequence analyses because they were uncorrelated ($p = 0.05$) to both the response variables (tree biomass, total forest floor thickness and post-fire forest floor thickness) and the independent variables (stand age, fire severity, and initial composition) (Table 3.1). This is probably a result of the general homogeneity of the landscape with respect to soil texture and slope, and of our selection of stands.

Total oven-dry tree biomass was estimated from the dbh of living trees > 2 m in height in the quadrats using allometric equations developed for the province (Ouellet 1983). Forest floor thickness was analysed both as the total thickness (from the mineral soil to the surface; "Total forest floor thickness") and as the portion that has accumulated since the last fire, i.e., excluding the residual organic matter (from the uppermost charcoal layer to the surface; "Post-fire forest floor thickness"). At the medium-term scale, the response variables (Tree biomass, Total forest floor thickness, Post-fire forest floor thickness) were analysed in a backward regression analysis with a linear model design (proc GLM, SAS/STAT statistical package version 8.0) using a combination of a continuous predictor variable (time since last fire; "TSF") and categorical predictor variables (initial stand composition, "COMP" and fire severity, "SEV"). Quadratic effects and interactions were included with the predictor variables in the initial model, but were removed when they were not significant (□ = 0.1). Because the design was incomplete (i.e., no *P. banksiana* stands originating from a LS fire), we excluded SEV*COMP interaction terms.

Among the 48 chronosequence stands, there were 4 pairs of young (< 100 years) *P. mariana* stands with each pair originating from the same fire event but differing with respect to the local severity of the last fire. These pairs were used to test the short-term (< 100 yrs) effects of fire severity on forest floor thickness and tree biomass using paired *t*-tests.

The effects of the extended absence of fire (> 250 yrs) on forest floor organic matter characteristics and biomass partitioning were assessed with linear regression (proc GLM, SAS/STAT statistical package version 8.0) following appropriate transformation of the predictor variable (Time Since Fire) to attain homoskedasticity and normality of residuals. Response variables using the forest floor survey data set include Upper and Lower Forest Floor Density, Forest Floor Biomass, and Total Ecosystem Biomass (Tree + Forest Floor biomass). All statistical analyses were performed with SAS – STAT statistical package (version 8.0).

3.5 Results

3.5.1 QMNR landscape survey

The comparison of stand characteristics of young (< 100 years) *P. mariana* and *P. banksiana* dominated stands on fine textured deposits within the QMNR database indicated that *P. banksiana* stands were more productive (tree basal area) and accumulated significantly thinner forest floors than *P. mariana* stands (Fig 3.2). The age and Slope Index of *P. banksiana* and *P. mariana* stands were not significantly different ($t = 0.61$, $p = 0.54$ and $t = 1.32$, $p = 0.19$ respectively; data not shown otherwise).

3.5.2 Chronosequence survey

When the severity of the last fire was taken into account, as was the case in the chronosequence survey, no significant difference between the composition types with respect to standing tree biomass and forest floor thickness was observed in the medium term (< 250 years) after HS fires (Table 3.2, Fig 3.3). On the other hand, the severity of the last fire significantly affected standing tree biomass, total forest floor thickness, and the thickness of forest floor organic matter accumulated since the last fire in black spruce dominated stands (Table 3.2, Fig 3.3). In the absence of fire, tree biomass peaked in stands established after HS fires at a higher value and at an earlier time than stands established after LS fires (Fig 3.3a). While the evolution of tree biomass was significantly affected by fire severity (severity * TSF interaction, Table 3.2), the amount of tree biomass in black spruce-dominated stands converged a few centuries after fire, regardless of fire severity (Fig 3.3a). Stands established after LS fires not only had a consistently

thicker forest floor than stands established after HS fires (Fig 3.3b), but they also accumulated forest floor organic matter at a quicker rate (severity * TSF interaction, Table 3.2, Fig 3.3c).

The analysis of the paired HS and LS sites, with each pair originating from the same fire, demonstrated similar results as LS stands accumulated nearly 50% thicker forest floor and 50% less tree biomass as compared to the stands established after HS fires (Table 3.3). No significant difference was observed ($p > 0.2$) between the paired sites with respect to soil topography and texture (data not shown).

After an initial burst and subsequent significant drop, tree biomass of *P. mariana* stands established after HS fires continued to decrease in the millennial absence of fire but at a much reduced rate (Fig 3.4a). Similarly, forest floor thickness, which increased significantly during the first couple of centuries, continued to increase in the long term but at a much slower rate (Fig 3.4b). Interestingly, forest floor thickness and standing tree biomass values for old stands (> 250 yrs) established after HS fires are similar to that of much younger stands (< 150 yrs) established after LS fires (Fig 3.4).

3.5.3 Forest floor survey

Forest floor characteristics significantly changed in the extended absence of fire and the Upper and Lower horizons within forest floor profiles evolved differently (Fig 3.5a). While the density of the lower forest floor layer significantly increased in the absence of fire, it slightly decreased in the upper forest floor layer. Consequently, although the accumulation of the forest floor organic matter measured as thickness appeared to slow down a few centuries after fire (Fig 3.4b), forest floor biomass increased linearly at a rate of 58 g m^{-2} yr^{-1} for numerous centuries after fire (Fig 3.5b). Total biomass (tree + forest floor pools) remained more or less constant for a few centuries after fire to subsequently increase exponentially (Fig 3.5b). Whereas ecosystem biomass may not have changed during the first few centuries after fire, the partitioning of this biomass among the tree and forest floor pools was significantly affected during this period (Fig 3.5b). Biomass in young stands was primarily (> 60%) locked-up in the tree pool, whereas it progressively became locked-up in the forest floor pool (> 80%) as succession proceeded.

3.6 Discussion

The discussion will first address the apparently conflicting results obtained with the two data sets with respect to the effects of the initial composition on standing tree biomass and forest floor thickness. We will then examine how the extended absence of fire and the severity of the last fire influenced ecosystem biomass partitioning. We conclude by discussing the effects of forest management practices and global climate change on the carbon source / sink capacity of the eastern boreal forest.

3.6.1 Initial tree composition

With the QMNR database, under similar abiotic conditions, *P. banksiana* stands appeared to accumulate less organic matter and produce more standing tree basal area than *P. mariana* stands. However, when the stand characteristics were compared between *P. mariana* and *P. banksiana* stands under similar abiotic conditions *and* after fires of comparable severity (chronosequence dataset), no significant difference in forest floor thickness or standing tree biomass emerged between the stand composition types. Fire severity had a significant effect however, with *P. mariana* stands established after LS fires showing thicker forest floors and lower standing tree biomass than stands established after HS fires. We therefore suggest that the apparent differences observed between stand composition types using the QMNR database is a result of the restriction of *P. banksiana*'s regeneration to sites with little ROM and the lack of qualification of fire severity during this survey. Studies probing the short term effects of residual organic matter (ROM) on post-fire regeneration have demonstrated that coniferous tree regeneration is negatively affected by an increase in the ROM thickness (Zasada and others 1983). However, *P. mariana* regeneration appears to be less affected than *P. banksiana*'s regeneration (Chrosciewicz 1974; 1976; Jeglum 1979). The scarcity of *P. banksiana* stands established after LS fires may also be a consequence of low post-fire seed availability, as some have suggested that LS fires are a result of long fire intervals that permit an excessive accumulation of forest floor humus (Foster 1985) and a replacement of *P. banksiana* by *P. mariana* after the first post-fire century (Lesieur and others 2002, Lecomte and Bergeron 2005, Chap1). These results, and the erroneous conclusions we would have drawn with the QMNR database, are a testimony to the

importance of qualifying the severity of the last fire to understand the full range of ecosystem processes occurring in the boreal forest.

These results contradict our hypothesis and previous reports, which stated that organic matter accumulation above the mineral soil is reduced while tree biomass production is enhanced in *P. banksiana* stands as compared to *P. mariana* stands (e.g. Gower and others 1997; Yu and others 2002; Miyanishi and Johnson 2002). As the severity of the last fire has rarely been taken into account in previous work in the boreal forest, these earlier reports may not have controlled sufficiently for fire severity and / or edaphic conditions. We postulate that under similar post-fire abiotic conditions, *P. mariana* stands may be as productive as *P. banksiana* stands, which reflects *P. mariana's* plasticity with respect to its ability to grow as an early successional fast-growing species and as a late successional slow-growing species (Dix and Swan, 1971). Furthermore, while we assumed black spruce litter decomposed at a slower rate than pine litter because of high litter C:N ratio and lignin content (Preston and others 2000), recent work over a 6 year period indicates that *P. mariana* needles may actually decompose as fast as *P. banksiana* needles despite having a higher lignin:N ratio (Trofymow and others 2002). In the end, the physiological plasticity of *P. mariana* and the slight differences in litter decomposition rates of the two species are probably the main reason we did not observe a difference in forest floor thickness and tree biomass dynamics between the composition types.

3.6.2 Extended absence of fire

As succession proceeds after HS fires, forest floors not only become thicker, but also denser because of compaction and humification of lower horizons. Although the accumulation rate of organic matter, measured as thickness, appears to slow down a few centuries after fire, it actually remains constant for numerous centuries after fire when expressed as dry biomass. Concurrently, after a peak in tree biomass a few decades after fire (80 years after HS fires), tree biomass declined rapidly during the following century and at a much reduced rate afterwards. Consequently, biomass partitioning is clearly regulated by the prolonged absence of fire. As succession proceeds, forest ecosystem biomass is progressively bound up in belowground biomass, while young stands have proportionately more biomass bound up in living trees. That the older stands contained

much higher belowground biomass levels than younger ones supports the notion that wild fire is of critical importance in reversing forest floor biomass lock-up in boreal forest ecosystems (Wardle and others 1997; O'Neill and others 2004; Van Cleve and Viereck 1981; Heinselman 1981).

The constant rate of forest floor biomass accumulation coupled with a drop in standing tree biomass (i.e. productivity) suggests that decomposition rates may not be constant through time in eastern boreal forests. Although there is little change in tree composition along the black spruce chronosequence, the bryophyte community shows a succession from a feathermoss-dominated community (primarily *Pleurozium schreberi*) to one that is dominated by *Sphagnum* species (Boudreault and others 2002), as others have reported in eastern North American boreal forests (Foster 1985; Taylor and others 1997). The presence of *Sphagnum spp* have been shown to affect water balance (Klenk 2001), lower soil temperatures (Van Cleve and Viereck 1981), reduce litter quality and consequently reduce decomposition rates (Zoltai and others 1998). Alternatively, the decrease in decomposition rates may be due to a positive feedback effect where the accumulation of forest floor humus, by dampening soil temperatures (Heinselman 1963; Swanson and others 2000; Klenk 2001; Fenton and others 2005a), simply lowers decomposition rates which maintains forest floor accumulation rates constant as tree productivity decreases.

The forest floor organic matter accumulation rates we report for *P. mariana* forests on the Clay Belt (58 g m^{-2} yr^{-1}) are closer to accumulation rates in North-American peatlands (bogs and fens) (Gorham and others 2003) than those reported for boreal forests (e.g. Wardle and others 2003). Gorham and colleagues (2003) compared peat accumulations rates in 32 sites from Alaska to Newfoundland and reported long-term rates that ranged from 16 to 80 g m^{-2} yr^{-1} with a median rate of 47 g m^{-2} yr^{-1} and a mean rate of 50 g m^{-2} yr^{-1}. Depending on the methods used to calculate accumulation rates, the authors reported rates between 54.6 and 62.2 g m^{-2} yr^{-1} for the one peatland site located near our study area (Lac Parent, Quebec 48° 47'N, 77° 10'W). The close agreement between these completely independent estimates of forest floor accumulation rates suggests that our chronosequence method of calculating peat accumulation in forested landscapes is valid.

The rate of carbon storage in the forest floor within the boreal zone of Sweden was estimated at about 5 g C m^{-2} yr^{-1} (Wardle and others 2003). Assuming that forest floor biomass is on average 40 to 50% made up of carbon in black spruce forests (Wang and others 2003; M. Simard, *unpublished data*) the reported rate of carbon accumulation in the forest floor organic matter for the Clay Belt would be close to 5 times higher than those reported for the boreal forest of Sweden. The higher rate of biomass accumulation and lock-up in the Clay Belt may be due to different understory compositions or to the underlying clay mineral soil. As mentioned above, along the black spruce chronosequence, the bryophyte community shows a succession from a feathermos-dominated community to one that is dominated by *Sphagnum* species. In the Swedish study no changes in non-vascular plant species was observed, with a constant dominance of *P. schreberi* throughout succession (Wardle and others 1997). The apparently higher rate of organic matter accumulation on the Clay Belt may also be due to the underlying clay mineral soil, that retains more water than the moranic deposits in the Swedish study, and may induce waterlogged conditions (Fenton and others 2005a). Excess soil water inhibits the exchange of oxygen and decomposition, which in turn favors the accumulation of forest floor biomass (Heinselman 1963). The progressive understory invasion by *Sphagnum* spp and the underlying waterlogged prone mineral soil are undoubtedly two main reasons forest floor accumulation rates in coniferous stands in the northern Clay Belt resemble rates encountered in peatlands more so than those found in boreal forests.

3.6.3 Fire severity and convergence

This study suggests that LS fires hamper the production of tree biomass, but enhance the accumulation of forest floor organic matter and thus influence ecosystem biomass partitioning. The similarity between very old stands (> 250 yrs) established after HS fires and the relatively young stands (< 150 yrs) established after LS fires with respect to thickness of forest floor organic matter and standing tree biomass suggests that LS fires do not fully reverse the biomass lock-up in forest floor organic matter observed in this landscape.

Although long term studies on the effects of fire severity on stand development are lacking, there are several studies on the effects of fire severity at shorter time scales

that might shed light on the processes that may be responsible for the significant differences observed between severity types. Partially burned residual organic matter has been shown to be a poor regeneration seedbed for most boreal tree species, reducing germination, early survivorship, and growth, compared to mineral or thin humus seedbeds (Chrosciewicz 1974; 1976; Zasada and others 1983; 1987; Charron and Greene 2002; Brais and others 2002). Furthermore, LS fires tend to favor understory species that possess an abundant buried propagule bank within the forest floor (Rydgren and others 2004; Schimmel and Granstrom 1996) notably the peat mosses (*Sphagnum* spp.) with their extraordinary ability to resprout from tissues deeply buried in the humus layer (Clymo and Duckett 1986, Dyrness and Norum 1983). The high cover of *Sphagnum* spp. after LS fires may have further depressed tree biomass production because tree growth is negatively affected by increases in the thickness of peat derived from *Sphagnum* spp. (Heinselman 1963). Since deep forest floors and *Sphagnum* spp. reduce decomposition rates, we postulate that these conditions, characteristic of young stands established after LS fires, are the main reasons forest floor biomass accumulation was enhanced and tree biomass was depressed after LS fires.

Our results demonstrate that in the short-term, fire severity induces a divergence in ecosystem biomass accumulation rate and relative partitioning among carbon pools. Nonetheless, the continual accumulation of organic matter and the drop in tree biomass observed after HS fires suggests that ecosystems, with respect to biomass dynamics, may converge in the extended absence of fire as noted for other ecosystem attributes in coniferous forest (Kashian and others 2005, Lecomte and Bergeron 2005, Chap 1).

3.7 Conclusion

This study demonstrates that *P. mariana* ecosystems established after HS fires continually accumulate biomass for numerous centuries after fire (> 700 years). After HS fires, ecosystem biomass partitioning was greatly altered as succession proceeded. Young stands had predominantly more biomass in living tree tissue while older stands had the majority of ecosystem biomass locked-up in forest floor organic matter. The post-fire dominance of *P. banksiana* had little effect on tree biomass production or forest floor thickness as compared to *P. mariana* stands. On the other hand, fire severity significantly

impacted tree productivity and forest floor thickness. The passage of LS fires favored the accumulation of thicker forest floors but lower standing tree biomass than HS fires, and therefore soil-burn severity significantly influenced ecosystem biomass partitioning

These findings, combined with the observed reduction in fire frequency since the end of the 'Little Ice Age' in the Clay Belt (*ca* 1850; Bergeron and others 2001), may have induced a significant amount of carbon sequestration within forest floors of coniferous stands on the northern Clay Belt. If current global climate change continue to induce even longer fire cycles in the eastern boreal forest (Flannigan and others 2001), the boreal forest on the Clay Belt of northwestern Quebec may continue to act as a significant carbon sink in the future. The results from this study illustrate that the effects of long fire-free periods and fire burn severity should be accounted for in eastern boreal forest carbon inventories and models.

These results also indicate that an increase in forest floor thickness may negatively impact tree productivity. This has led some including ourselves (Fenton and other 2005b) to suggest that in order to increase or maintain stand yield, forest managers in the Clay Belt should favor silvicultural approaches that remove a significant portion of the forest floor accumulated above the mineral soil (scarification, controlled burning). These approaches appear to make economic sense from a wood fiber production perspective. Nonetheless, from a climate change point of view, these approaches may prove very costly by releasing considerable amounts of carbon that has been sequestered in forest floor organic matter for centuries or even millennia. Careful studies should be undertaken to understand how current and alternative silvicultural practices might impact long-term carbon sequestration in the eastern boreal forest.

3.8 Acknowledgments

We thank Alayn Larouche and Hans Asnong for the laboratory analyses of forest floor monoliths and Marie-Éve Dion, Jean-François Giroux, Nathan Leverence, Simon Marcouiller, Guillaume Sauzède and Élise Vincent for their field assistance. Funding for this project was provided by the Industrial NSERC-UQAT-UQAM Chair in sustainable forest management and the Sustainable Forest Management Network and with graduate scholarships to the lead author from le Fond d'Action Québécois pour le Développement

Durable (FAQDD) and Le Fonds Québécois de Recherche sur la Nature et les Technologies (FQRNT).

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Appendix 3.A:

Site characteristics of stands from the chronosequence survey.

Site[a]	Initial composition[b]	*P. banksiana* basal area[c] (m^{-2} ha^{-1})	Relative abundance of *P. banksiana* macroremains[d]	Fire severity[e]	Residual OM[f]	Stand age			Mineral soil			Slope Index (°)[j]
						Oldest tree[g]	Calibrated ^{14}C age (charcoal)[h]	Calibrated ^{14}C age (humus)[i]	% sand	% silt	% clay	
30	Pine	29.5	88.5	High	1.2	45	-	-	1.5	22.0	76.5	1.0
54	Pine	43.6	92.5	High	1.0	51	-	-	0.0	12.7	87.3	1.9
61	Pine	32.5	77.1	High	1.5	51	-	-	6.5	21.5	72.0	5.1
36	Pine	39.4	63.2	High	1.6	76	-	-	1.0	23.6	75.4	0.6
38	Pine	23.1	75.2	High	1.6	84	-	-	0.0	9.0	91.0	0.7
23	Pine	32.0	63.1	High	1.3	86	-	-	3.5	26.9	69.7	1.4
57	Pine	34.2	57.2	High	1.2	88	-	-	13.0	45.5	41.5	1.2
29	Pine	39.9	44.3	High	1.2	135	-	-	19.9	30.8	49.3	1.2
69	Pine	34.2	40.7	High	1.1	139	-	-	2.0	34.3	63.7	1.9
66	Pine	28.5	36.4	High	1.7	149	-	-	12.5	25.0	62.5	8.7
73	Pine	50.8	27.9	High	1.3	149	-	-	26.0	25.0	49.0	1.5
40	Pine	35.6	28.6	High	1.1	151	-	-	25.5	27.5	47.0	2.4
49	Pine	28.4	35.7	High	1.2	155	-	-	14.0	63.0	23.0	2.1
94	Pine	44.7	36.0	High	1.0	176	-	-	6.0	24.5	69.5	5.1
83	Pine	40.0	61.7	High	1.0	177	-	-	4.0	20.0	76.0	1.0
79	Pine	20.1	16.0	High	1.1	179	-	-	2.4	29.0	68.6	0.0
65	Pine	32.8	8.8	High	2.1	204	-	-	14.0	32.5	53.5	0.8
64	Pine	25.8	2.6	High	1.9	222	-	-	0.0	38.4	61.6	3.9
67	Pine	15.2	0	High	1.0	229	-	-	0.0	28.6	71.4	1.4
62*	Spruce	0.0	0.0	High	1.4	52	-	-	2.0	23.4	74.6	10.5
4*	Spruce	0.0	0.0	High	2.5	53	-	-	0.0	38.1	61.9	2.5
59	Spruce	8.1	11.7	High	2.3	72	-	-	13.0	22.5	64.5	1.7
15	Spruce	2.4	30.3	High	1.5	76	-	-	10.3	27.9	61.8	-4.6
2*	Spruce	0.0	0.0	High	1.9	84	-	-	0.0	21.0	79.0	0.6
56	Spruce	0.0	0.0	High	1.3	86	-	-	13.5	28.5	58.0	0.8
12	Spruce	0.4	22.2	High	1.1	95	-	-	0.0	20.9	79.1	2.1
55*	Spruce	0.3	0.0	High	2.5	94	-	-	14.5	30.0	55.5	0.9
18	Spruce	0.0	0.0	High	2.0	126	-	-	15.0	18.0	67.0	1.8
75	Spruce	0.0	0.0	High	2.0	128	-	-	3.4	24.5	72.1	-1.3
8	Spruce	0.0	0.0	High	1.4	174	-	-	9.0	25.5	65.5	1.4
95	Spruce	0.0	0.0	High	1.3	184	-	-	3.0	26.0	71.0	1.7
9	Spruce	0.0	0.0	High	1.5	215	1225		11.5	23.5	65.0	1.6
7	Spruce	0.0	0.0	High	1.7	217	790	-	7.5	27.0	65.5	1.1
50	Spruce	0.0	0.0	High	2.0	222	365	-	19.0	27.0	54.0	1.3
6	Spruce	0.0	0.0	High	3.2	280	710	555	1.0	22.7	76.4	0.4
16	Spruce	0.0	0.0	High	2.7	286	1585	705	10.0	18.0	72.0	0.5
20	Spruce	0.0	0.0	High	3.2	353	2355	-	5.9	22.8	71.3	1.9
11	Spruce	0.0	0.0	Low	12.0	38	-	-	21.0	29.5	49.5	1.1
74*	Spruce	0.0	0.0	Low	13.0	52	-	-	6.0	26.5	67.5	1.3
53*	Spruce	0.0	0.0	Low	7.3	53	-	-	20.0	31.0	49.0	0.6
58	Spruce	0.0	0.0	Low	5.8	62	-	-	23.0	30.5	46.5	2.1
78	Spruce	0.0	0.0	Low	17.9	75	-	-	17.0	28.0	55.0	0.6
60*	Spruce	0.0	17.6	Low	6.7	84	-	-	9.0	15.0	76.0	1.2
3*	Spruce	0.0	0.0	Low	16.2	94	-	-	1.9	16.0	82.0	0.0
68	Spruce	1.6	4.9	Low	4.6	139	-	-	1.0	22.7	76.4	0.8
63	Spruce	0.0	0.0	Low	7.9	143	-	-	2.0	18.5	79.5	0.8
17	Spruce	0.0	0.0	Low	17.3	151	-	-	17.5	33.0	49.5	0.8
5	Spruce	0.7	0.0	Low	8.4	169	-	-	13.9	47.6	38.5	0.3

[a] Sites in boldface were part of the organic matter survey and a "*" denotes the paired sites originating after the same fire but differing with respect to fire severity

[b] Initial stand composition determined from the composition of dead and live trees as well as plant remains in forest floor profiles (see Methods).

[c] Total amount of live and dead *P. banksiana* stems > 2 m in height

[d] Abundance of *P. banksiana* macroremains in forest floor profiles relative to all tree macroremains found in the first 10 cm accumulated since the last fire (see Methods)

[e] Fire severity determined from the thickness of the residual organic matter (see Methods).

[f] Thickness of the residual organic matter, *i.e.*, the organic matter that was not burned by the last fire.

[g] Stand age determined from tree-ring analysis. Stands where the post-fire cohort of trees was not found were given a minimum age and were radiocarbon dated.

[h] Radiocarbon datings obtained from carbonized plant remains (see Methods).

[i] Radiocarbon datings obtained from humus accumulated just above the uppermost charcoal layer (from Cyr and others 2005).

[j] Slope Index integrates slope incline and landform shape, and can assume positive (mounds or regular slopes) or negative values (depressions) (see Methods)

3.10 List of figures

Figure 3.1. Classification of stands based on initial tree composition (a) and fire severity (b). A) Basal area of dead and live *P. banksiana* stems relative to stand basal area (all species, live and dead stems). Numbers in parentheses represent the number of data superposed at coordinates (0,0) for *P. mariana* high severity stands, and *P. mariana* low severity stands, respectively. B) Mean thickness of residual organic matter (ROM) obtained in the field and from detailed laboratory charcoal analysis.

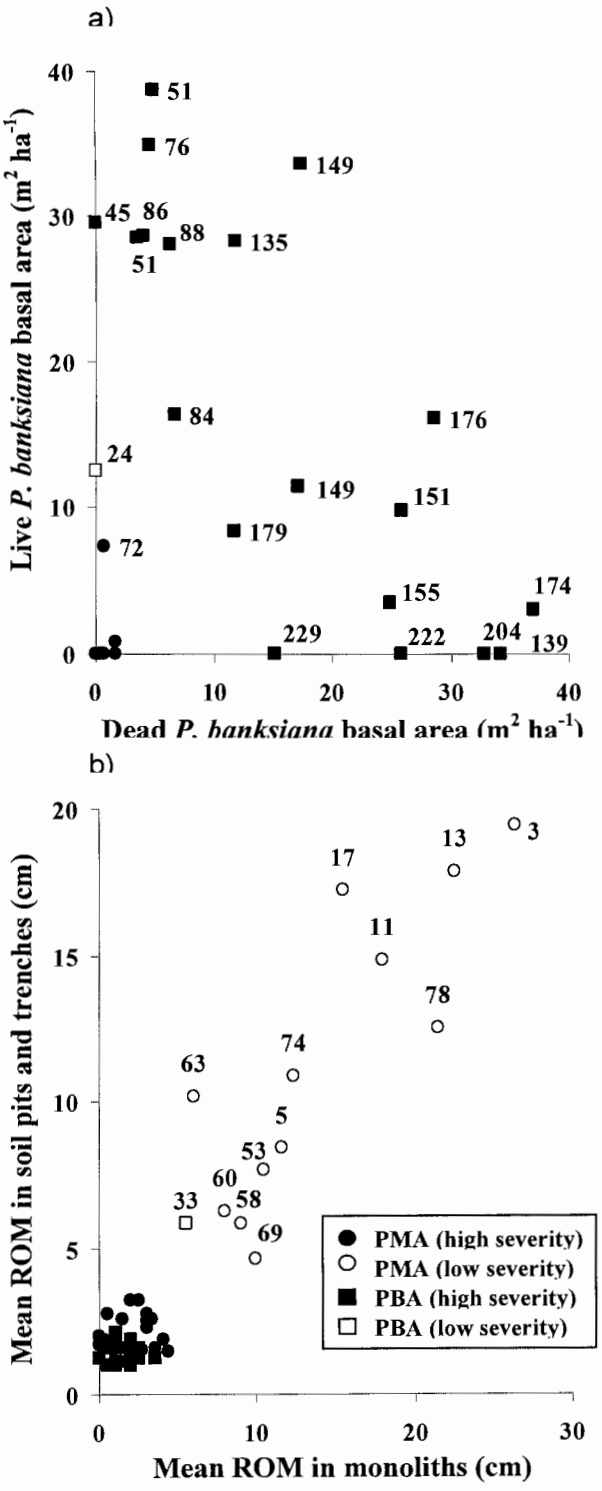
Figure 3.2. Basal area and total forest floor thickness of the two composition types (*P. banksiana* ($n = 18$) and *P. mariana* ($n = 84$)) from the QMNR database. Error bars are standard deviations.

Figure 3.3. Evolution of a) standing tree biomass, b) total forest floor thickness and c) post-fire forest floor thickness in relation to time since the last fire, using the medium term chronosequence dataset. Each symbol represents a stand ($n = 42$).

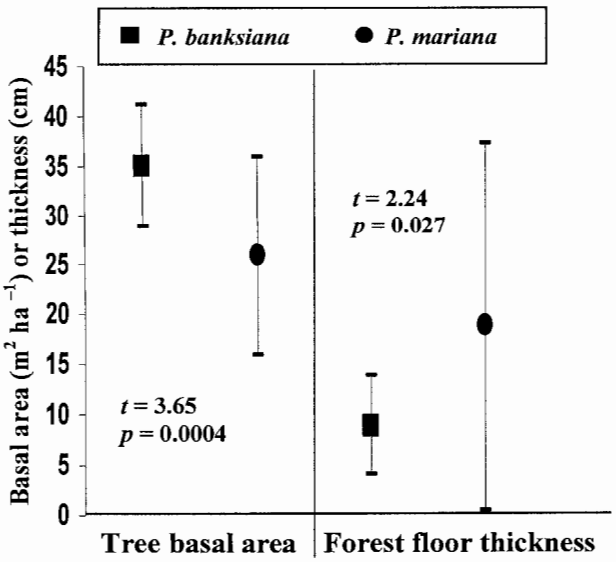
Figure 3.4. Evolution of a) standing tree biomass and b) total forest floor thickness with time since fire using the long-term chronosequence dataset. The regression equation between time since fire (TSF) and tree biomass ($BIOM_{TREE}$) is $\log BIOM_{TREE} = -0.209 \log TSF + 1.56$ ($R^2 = 0.46$, $P = 0.0019$), and between time since fire (TSF) and total forest floor thickness ($THCK_{FF}$) is $\log THCK_{FF} = 0.384 \log TSF + 0.509$ ($R^2 = 0.93$, $P < 0.0001$).

Figure 3.5: (A) Evolution of density of the forest floor in the Upper and Lower horizons. The regression equation between time since fire (TSF) and the density of the Upper forest floor horizon ($DENS_{UFF}$) is log $DENS_{UFF}$ = 0.00000151 TSF^2 –0.00159 TSF –1.12, and between time since fire (TSF) and the density of the Lower forest floor horizon ($DENS_{LFF}$) is log $DENS_{LFF}$ = 0.00000151 TSF^2 –0.000508 TSF –1.09 (R^2 = 0.64, $P < 0.0001$ for the full model). (B) Total forest floor biomass and total ecosystem biomass (tree + forest floor) using the forest floor organic matter data set. The regression equation between time since fire (TSF) and total forest floor biomass ($BIOM_{FF}$) is $BIOM_{FF}$ = 0.0581 TSF + 6.03 (R^2 = 0.92, P = 0.0002), and between time since fire (TSF) and total ecosystem biomass ($BIOM_{ECO}$) is B IOM_{ECO} = 0.0000651 TSF^2 + 25.5 (R^2 = 0.82, P = 0.0021).

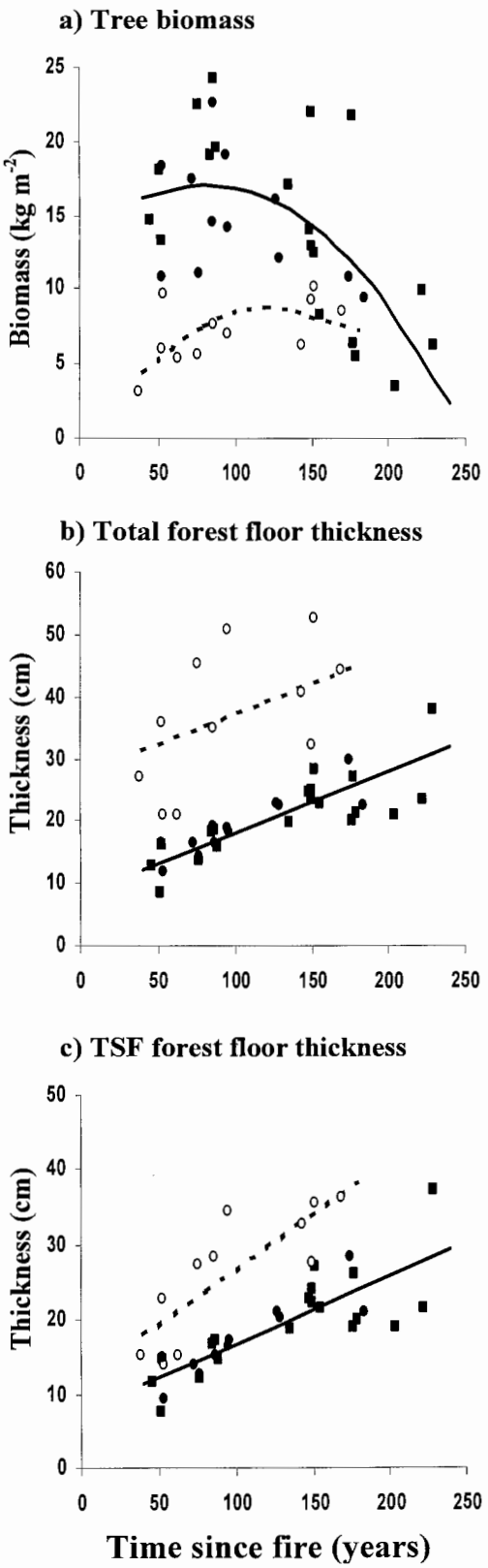
Figure 3.1


a)
Live P. banksiana basal area (m2 ha-1)
Dead P. banksiana basal area (m2 ha-1)
51
76
149
45
86
88
135
51
84
176
24
149
151
179
72
155
174
229
222
204
139
b)
Mean ROM in soil pits and trenches (cm)
Mean ROM in monoliths (cm)
3
13
17
11
78
74
63
5
53
60
58
33
69
PMA (high severity)
PMA (low severity)
PBA (high severity)
PBA (low severity)

1 **Figure 3.2**


P. banksiana
P. mariana
Basal area (m² ha⁻¹) or thickness (cm)
45
40
35
30
25
20
15
10
5
0
t = 3.65
p = 0.0004
t = 2.24
p = 0.027
Tree basal area
Forest floor thickness

1 **Figure 3.3**


a) Tree biomass
Biomass (kg m-2)
25
20
15
10
5
0
0
50
100
150
200
250
b) Total forest floor thickness
Thickness (cm)
60
50
40
30
20
10
0
0
50
100
150
200
250
c) TSF forest floor thickness
Thickness (cm)
50
40
30
20
10
0
0
50
100
150
200
250
Time since fire (years)

1 **Figure 3.4**

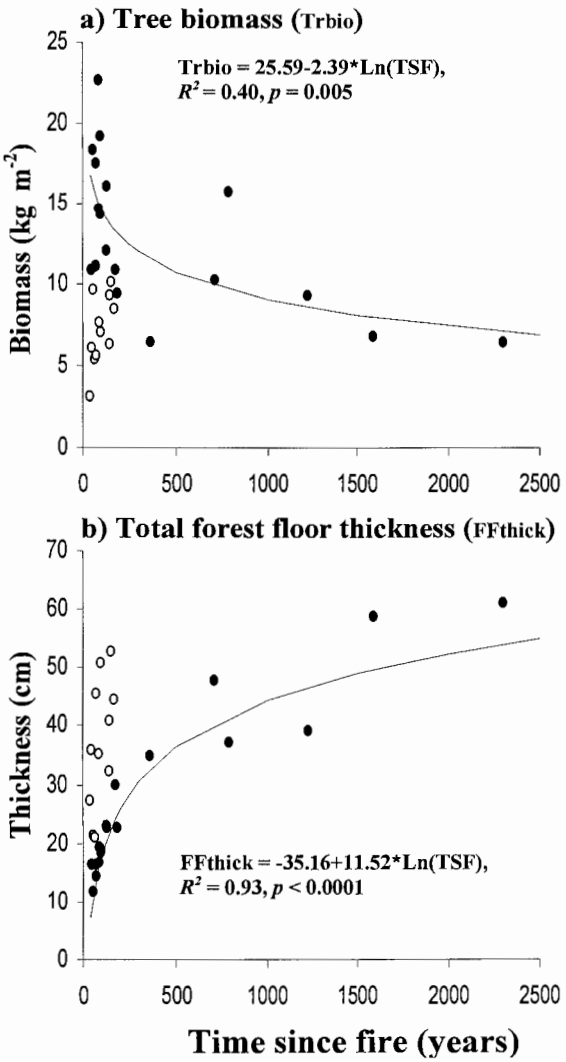

a) Tree biomass (Trbio)
Trbio = 25.59-2.39*Ln(TSF),
R^2 = 0.40, p = 0.005
Biomass (kg m^{-2})
0
5
10
15
20
25
0
500
1000
1500
2000
2500
b) Total forest floor thickness (FFthick)
FFthick = -35.16+11.52*Ln(TSF),
R^2 = 0.93, p < 0.0001
Thickness (cm)
0
10
20
30
40
50
60
70
Time since fire (years)

Figure 3.5

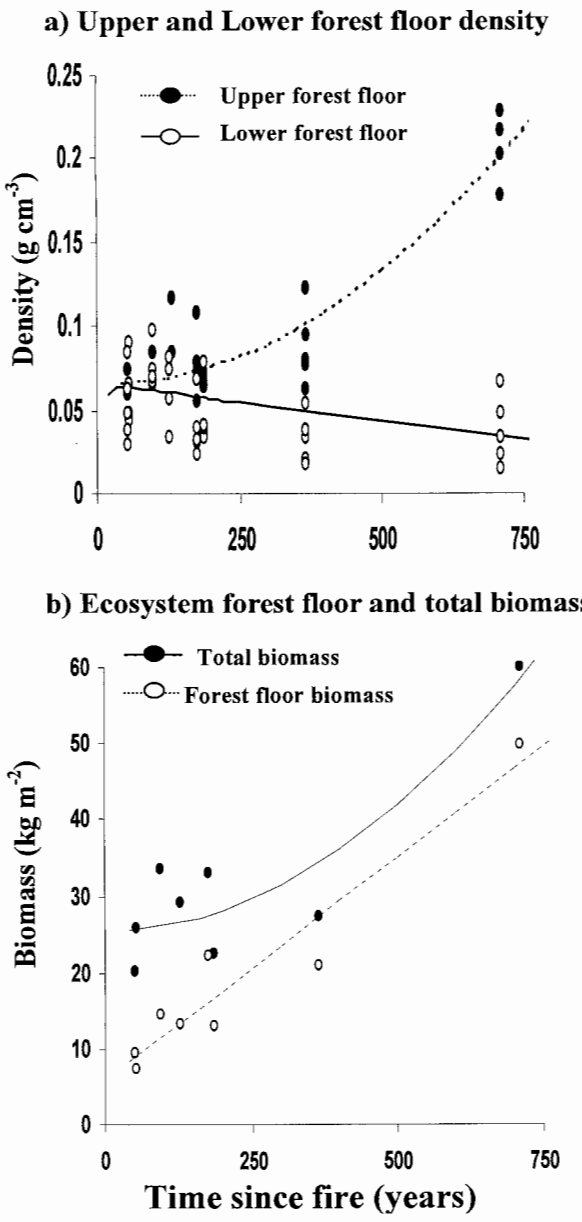

a) Upper and Lower forest floor density
Upper forest floor
Lower forest floor
Density (g cm-3)
0.25
0.2
0.15
0.1
0.05
0
0
250
500
750
b) Ecosystem forest floor and total biomass
Total biomass
Forest floor biomass
Biomass (kg m-2)
60
50
40
30
20
10
0
0
250
500
750
Time since fire (years)

Table 3.1.

Spearman (fire severity and initial composition) and Pearson (all other variables) correlations between the environmental variables, and the response and independent variables using the chronosequence dataset (n = 48).

	Environmental variables			
	Sand (%)	Silt (%)	Clay (%)	Slope Index (°)
Response variables				
Total forest floor thickness	-0.03	-0.12	0.10	-0.04
Post-fire forest floor thickness	0.01	-0.09	0.05	-0.12
Tree biomass	0.08	-0.07	0.00	-0.17
Independent variables				
Time since fire	-0.08	-0.08	0.10	0.12
Fire severity	-0.23	-0.07	0.10	0.28
Initial composition	-0.12	0.12	-0.04	0.26

Total forest floor thickness comprises both post-fire and residual forest floor organic matter.
For all correlations $p > 0.05$.

Table 3.2:

Results of General Linear Model for tree biomass and total and post-fire forest floor thickness using the medium term (< 250 yrs; $n = 42$) chronosequence dataset.

Response variables	Source	*F*	*P*
Tree biomass (kg m^{-2})	Initial composition (COMP)	-	N.S.
$R^2 = 0.58$	Fire severity (SEV)	15.01	**< 0.0001**
	Time since fire (TSF)	3.49	0.070
	COMP * TSF	-	N.S.
	SEV * TSF	2.89	0.098
	TSF * TSF	4.72	**0.036**
Total forest floor thickness (cm)	Initial composition (COMP)	-	N.S.
$R^2 = 0.74$	Fire severity (SEV)	93.54	**< 0.0001**
	Time since fire (TSF)	35.40	**< 0.0001**
	COMP * TSF	-	N.S.
	SEV * TSF	-	N.S.
	TSF * TSF	-	N.S.
Post-fire forest floor thickness (cm)	Initial composition (COMP)	-	N.S.
$R^2 = 0.74$	Fire severity (SEV)	1.69	0.201
	Time since fire (TSF)	63.87	**< 0.0001**
	COMP * TSF	-	N.S.
	SEV * TSF	3.51	0.069
	TSF * TSF	-	N.S.

Total forest floor thickness comprises both post-fire and residual forest floor organic matter.

Effects significant at the 0.05 and 0.1 level are in boldface and underlined, respectively.

Table 3.3

Paired *t*-tests for mean (± SD) total and post-fire forest floor thickness, and tree biomass with 4 pairs of *P. mariana* stands which originated from the same fire but differed with respect to fire severity. Data from the chronosequence survey.

Response variables	High severity	Low severity	*P*
Tree biomass (kg m^{-2})	15.4 (3.8)	7.6 (1.5)	**0.01**
Total forest floor thickness (cm)	16.5 (3.4)	35.7 (12.1)	**0.03**
Post-fire forest floor thickness (cm)	14.4 (3.6)	24.9 (8.8)	**0.04**

TSF, Time Since Fire
Total forest floor thickness comprises both post-fire and residual forest floor organic matter.
Significant effects ($p < 0.05$) are in boldface

CHAPITRE IV

Effects of fire severity and initial tree composition on understory vegetation dynamics in a boreal landscape inferred from chronosequence and paleoecological data

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4.1 Abstract

Question and Location: How does soil burn severity and early postfire tree composition affect long-term understory vegetation dynamics in the coniferous boreal forests of eastern Canada?

Method: Vegetation dynamics were assessed using paleoecological methods and a chronosequence analysis of extant stands. The importance of environmental factors on plant succession was evaluated using ordination techniques on the chronosequence data. Understory plant succession was studied 1) by using regression analysis on the chronosequence data and 2) by calculating within-site Markovian transition probabilities between successive 1-cm layers of plant macroremains from soil organic matter profiles.

Results: Initial tree composition (*Picea mariana* or *Pinus banksiana)* had little effect on understory composition. Soil burn severity (measured as the thickness of the residual forest floor humus) significantly affected temporal changes in understory species. Following fires of high severity, stands underwent a gradual paludification with a net increase in the abundance of *Sphagnum* species and evergreen ericaceous shrubs (*Ledum groenlandicum*), and an associated drop in the abundance of the feathermosses (*Pleurozium schreberi, Ptilium crista-castrensis*). Paludification was drastically accelerated after low severity fires which led to the dominance of Sphagnum less than 200 yrs after fire and *L. groenlandicum* shortly after fire. The description of *in situ* temporal changes in understory composition validated the results obtained with the chronosequence analysis.

Conclusions: Given the importance of fire severity, we demonstrate that one vegetation gradient related to time after disturbance is insufficient to account for the full complexity of long-term changes in understory composition following fire. Our results suggest that current forestry practices that protect the forest floor humus may induce a premature paludification of stands and decrease in stand productivity.

Keywords: boreal forest, disturbance, residual organic matter, succession, paludification, ericaceous shrubs, *Sphagnum* spp., Feathermosses, *Picea mariana* (black spruce), *Pinus banksiana* (jack pine), plant macrofossil analysis.

Abbreviations: HS = High Severity; LS = Low Severity; GCC = Global Climate Change; TSF = Time Since last Fire

Nomenclature: Marie-Victorin (1995) and Montgomery (1977) for vascular plants; Anderson et al. (1990) for bryophytes and Lévesque et al. (1988) for macrofossils. Several species are treated collectively.

4.2 Résumé

Question et Site: Comment est-ce que la sévérité du feu et la composition initiale affecte la dynamique à long-terme dans la forêt boréale de l'Est du Canada.

Méthode: La dynamique de la végétation a été déterminée en utilisant une approche qui a combiné des méthodes paléoécologiques à l'analyse d'une chronoséquence de peuplements. L'importance des facteurs environnementaux sur la succession végétale a été évalué en utilisant des ordinations. La succession en sous-bois fut étudié 1) n utilisant des analyses de régression ett 2) en calculant des probabilités Markoviennes de transition entre des couches successive se retrouvant au sein des profils de matière organique accumulée au sol.

Résultats: La composition initiale, dominée soit par *Picea mariana* ou *Pinus banksiana,* a eu peu d'effet sur les changements de composition dans le sous-bois. Toutefois, la sévérité du dernier feu a affecté significativement les changements temporels dans la communauté vasculaire et invasculaire du sous-bois. Suite à des feux sévères, les peuplements forestiers ont connu un entourbement graduel avec une augmentation dans l'abondance de *Sphagnum* spp. et des arbustes éricacées (*Ledum groenlanndicum*) et une baisse dans l'abondance des mousses hypnacées (*Pleurozium shreberi, Ptilium crista-castrensis*). En inhibant la régénération après feu et la fermeture de la canopée, les feux

de faible sévérité accélèrent le taux d'entourbement avec une colonisation précoce des peuplements par *L. groenlandicum* et un remplacement des mousses hypnacées par *Sphagnum* spp. La stratigraphie des macrofossiles végétaux dans les profils de matière organique a confirmé que la mosaïque des communautés successionelles au sein de ce paysage représente des analogues pour les changements temporels dans un site à condition que la sévérité du dernier feu soit prise en compte.

Conclusions: Étant donné l'importance de la sévérité du feu, nous démontrons qu'un seul gradient relié au temps depuis la dernière perturbation est insuffisant pour expliquer la complexité des changements à long terme dans la communauté de sous-bois. . Nos résultats suggèrent que les approches sylvioles actuelles qui protégent la matière organique accumulée au sol pourrait accéléer le processus d'entourbement et la perte de productivité

Mot clefs: forêt boréale, perturbations, communauté de sous-bois, sévérité du feu, succession, entourbement, *Sphagnum spp.*, mousses hypnacées, *Picea mariana* (épinette noire), *Pinus banksiana* (pin gris), analyse des macrofossiles végétaux

4.3 Introduction

Although boreal forest understory species represent a small fraction of the above-ground living biomass, they often make up a significant portion of stand net primary production and may even out-produce overstory tree species (Chapin 1983; O'Connell et al. 2003). The continuous ground cover of non-vascular species that characterises boreal forests (Oechel & Van Cleve 1986) affects soil thermal regimes, nutrient availability and tree productivity (Heinselman 1963; Van Cleve & Viereck 1981). Ericaceous shrubs can influence ecosystem processes such as nutrient cycling and have a detrimental effect on tree growth (e.g., Inderjit & Mallik 1997; Nilsson et al. 1993). Given the importance of understory species to the functioning of boreal ecosystems, it is important to understand how environmental gradients determine the distribution of these species within landscapes.

Even under similar abiotic conditions, multiple successional trajectories in overstory tree composition and structure can co-occur within boreal forest landscape (e.g., Payette et al. 2000, Lesieur et al. 2002; Lecomte et al. 2006, Chap 2). This co-occurrence can be strongly linked to site-specific historical fire regimes (Larocque et al. 2000; Johnstone & Chapin 2005). Short fire intervals tend to favour tree species that reach sexual maturity quickly (e.g., *Pinus banksiana* in eastern North America) while longer fire cycles will tend to favour longer-lived species or species that are able to regenerate in the absence of fire (e.g., *P. mariana*). Long fire cycles that characterise eastern Canadian boreal landscapes (Bergeron et al 2004a; Foster 1985) cause a high proportion of low severity fires that do not fully consume the thick forest floor that has accumulated during long fire-free intervals (Foster 1985; Simon & Schwab 2005). Fire severity affects tree regeneration and hence stand structural development (Foster 1985; Lecomte et al. 2006, Chap 2). Global climate change (GCC) will undoubtedly affect fire regimes (Flannigan et al. 2001; Bergeron et al. 2004a) and in turn the frequency of overstory successional trajectories and fire severity types. Hence, understanding how GCC may influence the distribution of understory species necessitates the comprehension of how the abundance of these species varies along multiple overstory successional series co-occurring within a landscape under similar topo-edaphic conditions.

To circumvent the problem of long time-spans in studying boreal forest vegetation

dynamics, the chronosequence approach has been often used to study changes in understory composition (e.g., Taylor et al. 1987; Wang et al. 2003). The major drawback of this approach resides in the uncertainty that the selected stands have experienced the same history, due to perhaps differences in fire behaviour, pre-burn composition and/or initial understory composition. The use of paleoecological methods to determine past vegetation and fire severity in individual stands forming the chronosequence addresses some of the shortcomings associated with time-series analyses. In boreal forests, under moist, cool and acid conditions unfavourable to decomposition processes, plant remains are gradually incorporated in the organic soil layer as stands age. The stratigraphic analysis of partially or undecomposed plant detritus (macroremains) within forest floor profiles can reveal temporal changes in understory composition since the last fire as well as the fire's severity (Foster 1985; Ohlson et al. 2001).

In this study, we investigated how the initial tree composition and the severity of the last fire influenced long-term changes in understory species composition of coniferous boreal stands. Here, we refer to fire severity exclusively as the effects of fire on the accumulated soil organic matter (quantity of duff burned / quantity of duff unburned *sensu* Miyanishi & Johnson, 2002) as opposed to the effects of fire on the canopy (% trees killed; *sensu* Greene *et al.*, 2004). Temporal changes were analysed along three chronosequences of stands that showed contrasting fire history and initial postfire tree composition: *Pinus*-dominated stands after high severity fires, *Picea*-dominated stands after high severity fires, and *Picea*-dominated stands after low severity fires. While temporal changes in understory composition have been documented along boreal stand chronosequences (e.g., Foster 1985; Taylor et al. 1987; De Grandpré et al. 1993; Wang et al. 2003) few if any studies have compared changes in understory vegetation composition along multiple overstory successional series. Also, while the short-term influences of fire severity on understory species composition have been studied (e.g., Schimmel & Granström1996; Nguyen-Xuan et al. 2000; Rydgren et al. 2004), to our knowledge no study has compared long-term successional changes occurring after high and low severity fires. Temporal trends observed with time series analysis were compared to those observed with macrofossil analyses of forest floor profiles from all study sites.

Since *Pinus*-dominated stands transmit more light to the understory (Messier et al. 1998; Légaré et al 2001) and produce litter with higher N-content (Preston et al. 2000) as compared to *Picea*-dominated stands, we hypothesise that the initial postfire dominance of *Pinus* favours shade-intolerant and nutrient-demanding understory species. As low severity fires favour species that were present in the preburn stand (Schimmel & Granström 1996; Nguyen-Xuan et al. 2000; Rydgren et al. 2004), we hypothesise that a low fire severity accelerates the rate of successional change in understory composition compared to high severity fires.

4.4 Methods

4.4.1 Study area

The study area (49ºN to 51º 20'N; 78º 30'W to 79º 50'W) is located within the Clay Belt of northeastern Ontario and northwestern Quebec, Canada and is within the *Picea mariana*—feathermoss bioclimatic domain (Robitaille & Saucier 1998). The Clay Belt is a physiographic unit composed mostly of clay deposits left by pro-glacial Lake Ojibway (Veillette 1994). Although a few rocky outcrops are present, the topography is generally flat. Average annual temperature (1971-2000) at the closest weather station to the North (Matagami, 49º 46'N, 77º 49'W) and South (La Sarre, 48º 46'N, 79º 13'W) of the study area are respectively –0.7 º C and 0.7 º C with an average of 906 mm and 890 mm of precipitation annually (Environment Canada 2005). Most of the area is covered by structurally diverse coniferous forests dominated either by *Picea mariana* or *Pinus banksiana* (Lecomte and Bergeron 2005, Chap 1) with a forest floor dominated either by *Sphagnum spp.* or *Pleurozium schreberi* (Boudreault et al. 2002). Occasional deciduous stands are dispersed across the landscape. Although agricultural settlement south of the study area began in the middle of the 1930s, intensive logging of this area commenced in the late 1970s. Fire is the main disturbance that terminates and initiates secondary successions. Fire cycle length has increased from 101 years before 1850, to 398 years since 1920; with mean stand age currently 148 years (Bergeron et al. 2004b).

4.4.2 Field and laboratory analyses

In this study we sampled 48 stands which differed with respect to the severity of the last fire, the time since the last fire and the initial tree composition after fire, but showed similar mineral soil texture and slope (Appendix 4.A). Initial tree composition was evaluated based on current composition of live and dead stems (including buried stems). Stand age (fire year) was determined by carefully dating cross-sections taken at the base of live and dead dominant trees. In stands where the oldest tree exceeded 200 years, and no fire scars or pioneer species (*Pinus banksiana*) were present, samples of carbonised plant remains found in soils were AMS radiocarbon-dated. The severity of the last fire for each stand was qualified as high (HS) or low (LS) based on the average thickness of the residual organic matter present in the stand (*i.e.*, the soil organic matter that was not burned by the last fire). At each stand, understory vegetation was assessed in ten 1-m^2 square plots. *In situ* temporal changes in understory composition was evaluated by determining the abundance of plant macroremains found in forest floor humus monoliths taken at each stand (two to three monoliths per stand). For detailed methods please consult Appendix 4.B and Lecomte et al. (2006).

4.4.3 Statistical Analyses

4.3.3.1 Chronosequence dataset

To evaluate the factors responsible for the variation in forest understory plant communities, the mean abundance of each taxa in the chronosequence stands were used to compute a canonical correspondence analysis (CCA) using the program CANOCO Version 4 (Ter Braak & Šmilauer 1999). The continuous environmental variables (mineral soil clay content, Slope Index and time since fire (TSF)), and categorical variables (fire severity and initial stand composition) were loaded by forward selection. Additionally, we were interested in how initial stand conditions influenced vegetation dynamics so we included the two following interactions: TSF * fire severity and TSF * initial stand composition. Significance of each variable was computed using a Monte Carlo test ($\alpha = 0.05$). Only the 17 species or groups of species occurring in over 10% of the 1 m^2 plots were used for the CCA (Appendix 4.C). Finally, to examine the

relationship between understory species and temporally varying stand characteristics, we entered *a posteriori* (passively) in the CCA the following stand variables: forest floor thickness and total stand basal area represented by large stems (dbh > 10 cm).

The quantitative effect of fire severity and initial composition on understory composition was assessed in the chronosequence stands using the abundance of the three dominant terricolous bryophyte and lichen taxa (*Sphagnum* spp., Feathermosses, and *Cladina* spp.) and the two most abundant shrub taxa (*Ledum groenlandicum* and *Vaccinium* spp. (*V. angustifolium* and *V. myrtilloides*)) as response variables. Since the CCA showed that slope and soil texture were not significant in explaining understory composition, we have not included them in the analyses. As the three chronosequences, based on initial composition and fire severity, spanned different time scales (*Pinus banksiana* HS: 45 – 229 years, *Picea mariana* LS: 38 – 169 years, and *Picea mariana* HS: 50 - 2355 years), the data were analysed at two distinct time scales: medium term [< 250 years] and long term [> 250 years]. The medium term scale permitted us to assess the effects of both fire severity and initial stand composition on understory species composition. The long-term scale allowed us to evaluate how the understory composition of *Picea mariana* stands established after HS fires evolved in the extended absence of fire.

Medium-term effects were assessed with a Linear Model design (PROC GLM, SAS Institute 2000) with a combination of a continuous predictor variable (TSF) and categorical predictor variables (initial stand composition and fire severity). When predictor variables or interaction were not significant ($p > 0.05$) they were removed from the models. The quantitative effects of the long-term absence of fire on understory composition were assessed with linear regression following appropriate transformation of the independent variable (TSF).

4.4.3.2 Organic matter monoliths

The vegetation changes that occurred since the last fire were assessed using Markovian transition probabilities. Using only horizons that had been accumulated since the last fire, the probabilities were computed from observed changes in abundance of plant macroremains and dead wood from one organic matter horizon (1-cm thick) to the next. Only ground species (*Sphagnum* spp., Feathermosses (*Pleurozium schreberi*,

Ptilium crista-castrensis, *Hylocomium splendens*), *Polytrichum* spp., *Dicranum* spp., and Lichens) were considered, as they represented the majority of plant remains identified within the monoliths. Transition probabilities were separately calculated for each chronosequence, and for three different time scales: stands less than 100 years old, stands > 100 years old, and all stands. The 100 year cut-off was used because stands colonising LS fires remain open throughout succession while comparable stands established after HS fires rapidly close and then open their canopies after 100 years (Lecomte et al. 2006) (Chap 2).

4.5 Results

4.5.1 Chronosequence survey – Ordination trends

The CCA with the 48 stands demonstrated that 1) the canonical axes 1 and 2 explained respectively 14% and 10% of the variance in species composition and 2) the environmental variables, fire severity, Time Since Fire (TSF) and the interaction fire severity * TSF, each explained 6% of the variation (Table 4.1). All other environmental variables and interactions did not significantly ($p > 0.05$) explain any more of the among-stand understory composition variability.

The ordination diagram indicates that axis 1 is mainly linked to a paludification gradient, as reflected by the positive association of the environmental variables TSF and total organic matter thickness along with the hydrophylous species, *Sphagnum* spp., *Smilacina trifolia,* and *Equisetum sylvaticum* (Figure 4.1A). Axis 2 is negatively associated with fire severity and total basal area represented by large stems as well as with a cluster of species associated with shaded conditions (*Pleurozium schreberi*, *Dicranum* spp., *Ptilium crista-castrensis, Petasites palmatus*, *Cornus canadensis* and *Maianthemum canadense).* Axis 2 is also positively associated with species typical of xeric and/or high light environments such as the ericaceous shrubs (*Vaccinium* spp., *Kalmia angustifolia* and *Ledum groenlandicum*) and *Cladina* spp. The considerable length of the vectors representing the varying stand structural attributes (canopy closure and forest floor thickness) is a testimony to the strong relationship between these variables and understory composition.

The successional vectors, which connect the mean ordination score for each stand age-class, suggest that the understory composition of stands evolving after HS fires gradually shifted from an assemblage of species strongly associated with shaded conditions to one that is strongly associated with wet conditions (Figure 4.1B). The large overlap between identical age-class ellipses of the two composition types evolving after HS fires indicates that the initial composition (*Pinus banksiana vs Picea mariana*) had little effect on understory composition (Figure 4.1B). The *Pinus banksiana* vector is shorter as we did not sample any old stands (> 250 years) that were postfire dominated by *Pinus banksiana* (Figure 4.1B). The successional vector of stands evolving after low severity (LS) fires indicates that these stands underwent a change in understory composition from species associated with high light and xeric environments to species strongly associated with wet conditions (Figure 4.1B). The lack of overlap between identical age-class ellipses of the two severity types suggests that fire severity greatly influenced understory composition. However, the near perfect overlap of the 100-250 year old age-class ellipse of the LS fire chronosequence and the oldest age-class ellipse of the HS fire *Picea mariana* chronosequence suggests that 1) fire severity accelerated the rate of paludification in this landscape and that 2) the prolonged absence of fire induced a convergence in understory composition regardless of the severity of the last fire.

4.5.2 Chronosequence survey – Quantitative trends in understory composition

The initial composition did not significantly affect temporal changes in abundance of the main understory species (Table 4.2). In contrast, fire severity significantly affected the evolution in the abundance of all taxa (Table 4.2, Figure 4.2). After HS fires, while *Sphagnum* and ericaceous shrubs became more abundant, the abundance of feathermosses decreased, while few temporal changes were observed in the cover of *Cladina* spp. (Figure 4.2). In contrast, LS fires appeared to accelerate the replacement of feathermosses by *Sphagnum* and initially favoured the presence of *Cladina* and *Vaccinium*, which eventually decreased in the absence of fire (Figure 4.2). While fire severity did not affect the rate of change in the abundance of feathermosses and *L. groenlandicum* (no TSF * Severity interaction), the feathermosses were initially less abundant and *L. groenlandicum* more abundant after LS fires than after HS fires.

In the extended absence of fire (> 250 years), after HS fires, the trends observed during the first few centuries resumed with a continued increase in the cover of *L. groenlandicum* and a decrease in the abundance of the feathermosses (Figure 4.3). Although *Sphagnum* abundance significantly increased in the absence of fire and was present in all the stands older than 250 years, it showed a large variability among the oldest stands. Although, we observed a significant relationship between *Cladina* spp. cover and TSF, this was mostly due to the higher cover of this species in only the oldest stand. No significant trend in the cover of *Vaccinium* species was observed with a relatively constant low cover (< 10%). Notably, the abundance of the five main understory taxa in stands evolving after LS fires resembled the cover values of these species in much older stands evolving after HS fires (Figure 4.3).

4.5.3 Organic matter monoliths – In situ temporal changes in understory composition

The soil monoliths showed organic matter accumulations since the last fire ranging from 2 cm to 56 cm (mean = 14.1 cm; S.D. = 9.5 cm). The transition matrices showed considerable differences between stand age classes and fire severity types (HS *vs* LS in *P. mariana* stands), but few differences between overstory tree composition (*Pinus banksiana* vs *Picea mariana* in HS fires) (Appendix 4.D, Figure 4.4). In young HS stands (< 100 years), all ground species showed a high probability of being replaced by feathermosses while in the prolonged absence of fire (stands > 100 years) species in general demonstrated a higher probability of being replaced by *Sphagnum* (Figure 4.4). The transition probabilities are thus not stable in time after HS fires. In contrast, ground species in LS stands consistently showed high transition probabilities toward *Sphagnum* regardless of the age classification of stands (Figure 4.4). In all stands, *Sphagnum* always showed a strong positive feedback, i.e., a strong tendency for self-replacement. In general, *Polytrichum*, *Dicranum,* and Lichen species showed a low probability of replacing other species and a high probability of being replaced by either *Sphagnum* spp. or feathermosses, reflecting their early successional status in this landscape.

4.6 Discussion

4.6.1 Initial tree composition

Our results contradict the hypothesis that overstory composition (*Pinus* vs *Picea*) affects understory composition (Légaré et al. 2001; Yu et al. 2002). In the eastern Canadian boreal forest, shortly after the first postfire century, *Picea mariana* replaces *Pinus banksiana* (Lesieur et al. 2002; Lecomte and Bergeron 2005, Chap 2). Viereck (1983) demonstrated that in boreal coniferous stands, the main factors influencing the forest floor environment were changes in canopy closure and the accumulating forest floor with time. In this landscape prone to paludification, after HS fires, initial overstory composition does not influence the evolution of stand canopy closure or thickness of the forest floor (Lecomte et al. 2006, Chap 2). While nitrogen concentrations in *Pinus* litter have been found to be higher than in *Picea* litter (Preston et al. 2000), no significant difference in their decay rates have been observed over a six-year period (Trofymov et al. 2002). In the end, the short duration of *P. banksiana*'s domination and the minimal effect of its dominance on canopy closure, forest floor thickness or potential litter decomposition are probably the main reasons an initial *Pinus banksiana* dominance had no significant effect on understory composition.

4.6.2 Temporal changes after high severity fires

After HS fires, the most important successional change in understory composition is the shift in dominance from feathermosses in young postfire stands to *Sphagnum* spp., which is concurrent with a gradual increase in organic matter thickness and opening of the canopy. After HS fires, high stem density and rapid growth leads to the rapid closure of the canopy (Lecomte et al. 2006 Chap 2; Taylor et al. 1987). However, as stands reach 100 years, the canopy gradually opens (Lecomte et al. 2006, Chap 2) in response to secondary disturbances (insect, pathogens, windthrow) and senescence . In the extended absence of fire, the continual thickening of the forest floor lowers tree productivity (Heinselman 1963), which inhibits a 'reclosure' of the canopy after the postfire tree cohort dies (Boudreault et al. 2002; Lecomte et al. 2006, Chap 2). The opening of the canopy greatly modifies the light/moisture environment of the understory, and consequently the abundance of bryophyte and vascular understory species. Feathermoss ground cover competing with *Sphagnum* spp. is positively associated with overstory canopy closure (Bisbee et al. 2001), a relationship that is likely caused by the different

mechanisms by which these species can acquire moisture. While dew formation and precipitation are important sources of moisture for feathermosses, *Sphagnum* spp. can wick up water through the forest floor from the water table (Busby and Whitfield, 1978). A gradual thickening of the forest floor causes the water table to rise above the forest floor-mineral soil interface, which makes water more accessible to *Sphagnum* spp. (Fenton et al. *accepted*). Our results suggest that the replacement of feathermosses by *Sphagnum* spp. as succession proceeds past the first century, reflects the differential response of species to the temporally varying closure of the canopy and thickness of the forest floor. These results are consistent with the ecophysiological requirements of these species and previous reports in the boreal forest (Groot and Horton 1994; Taylor et al. 1987; Boudreault et al. 2002).

The increase in understory shrub cover (*Vaccinium* spp. and *Ledum groenlandicum*) probably reflects the response of these shade-intolerant species to the gradual opening of the canopy. However, the greater increase in the cover of the evergreen shrub *L. groenlandicum* as opposed to the deciduous shrubs (*Vaccinium* spp.) may reflect the effects of the temporally varying availability of nutrients on these species. Deciduous shrubs frequently occur on more fertile sites than evergreen shrubs due to their greater annual nutrient demand (Chapin 1980). As stands mature and forest floors thicken, soil pH and temperatures decrease, which slows down decomposition rates and reduce nutrient availability (Viereck 1983). We postulate that the lower availability of nutrients as stands mature gives a competitive advantage to evergreen nutrient-conserving shrub species over deciduous nutrient-demanding species (Groot and Horton 1994; Wardle et al. 1997).

Our results suggest that after HS fires long fire-free intervals, by influencing ecosystem characteristics such as light transmittance and forest floor depth, greatly affect understory composition. In the absence of fire, the opening of the canopy and the gradual thickening of the forest floor, coupled with an increase in the cover of *Sphagnum* spp. and evergreen shrubs demonstrate the prevalence of paludification in the Clay Belt (Taylor et al. 1987; Heinselman 1981; Boudreault et al. 2002).

4.6.3 Temporal changes after low severity fires

acceleration of the paludification process. This suggests that even under similar abiotic conditions, one vegetation gradient related to time after disturbance is insufficient to account for the full complexity of long term vegetation processes following fire in the coniferous boreal forest and that fire severity should be considered.

4.6.4 Paleovegetation and chronosequence results

The stratigraphy of plant remains within soil organic matter profiles confirmed that the mosaic of successional communities observed across this landscape provides analogues for the temporal sequence at individual stands if the severity of the last fire is accounted for. Both chronosequence and paleoecological data sets document the replacement of feathermosses by *Sphagnum* spp. in the absence of fire. Both indicate few differences in understory dynamics between the *Pinus banksiana*- and *Picea mariana*-dominated stands and a premature replacement of feathermosses by *Sphagnum* spp. after LS fires. The stratigraphic history of fire severity and of vegetation change since the last fire at each stand strengthens the conclusions that are drawn from the detailed analysis of the chronosequence stands.

4.6.5 Landscape variability in understory vegetation, current forestry practices and GCC

Among-stand variability in understory composition within this boreal landscape was related to temporal changes in stand structural attributes occurring in the absence of fire and by initial stand conditions. However, differing initial coniferous tree compositions did not significantly affect understory composition. LS fires, by favouring late-successional species and hampering canopy closure, induced a premature paludification of coniferous boreal stands on fine-textured deposits. Hence, by highlighting the important effects of fire interval and severity on understory composition, we have demonstrated that changes in disturbance regime may have important effects on the distribution of understory species within the Clay Belt of eastern Canada. Furthermore our results indicate that the use of paleoecological methods along a chronosequence of stands represents a multi-proxy approach which provides a novel and robust way of studying vegetation dynamics occurring over several centuries.

The thick residual organic matter left after the passage of a LS fire negatively influences postfire tree regeneration (Greene 2004), subsequent nutrient availability (Van Cleve and Dyrness 1983), and tree growth (Zasada et al. 1987). Stand development after LS fires is characterised by the maintenance of an open canopy and a consistently thicker forest floor as compared to HS fires (Lecomte et al. 2006, Chap 3). The maintenance of an open canopy during stand development after LS fires induces a rapid invasion of the site by species tolerant of high light / xeric conditions such as the terricolous lichens *Cladina* spp. Then as the forest floor thickens the non-vascular plant community rapidly becomes dominated by *Sphagnum* spp.

The early dominance of the understory of stands established after LS fires by *Cladina* spp is consistent with observations from Labrador in eastern Canada which documented the evolution of the understory composition in *P. mariana*-dominated stands after LS fires (Foster 1985; Simon and Schwab 2005). However, while these authors reported a gradual replacement of the *Cladina* lichens by feathermosses, we observed a rapid invasion of the stands by *Sphagnum spp*. These differing understory trajectories may be due to the fact that the Labrador stands were established on coarse-textured morainic deposits unlike the fine-textured glaciolacustrine deposits on the Clay Belt. The lower water holding capacity of the coarse textured deposits may have hampered the accumulation of forest floor organic matter and favoured tree growth, canopy closure and hence the feathermosses over *Sphagnum*. Furthermore, the authors of the Labrador studies reported a gradual closure of the canopy late during the first century after fire, which was to some degree accomplished by the establishment of *Abies balsamea*. However this fire-avoider species is scarce in the Clay Belt, probably because of the fire regime that is characterised by large fires (Bergeron et al. 2004b). Large fires tend to leave a lower quantity of green trees inside the fire perimeter, which greatly reduces the post fire establishment of *A. balsamea*.

The deeply buried reproductive organs of the ericaceous shrubs species (Flinn and Wein 1977) give them an advantage after the passage of a LS fire (Nguyen-Xuan et al. 2000). Far more individuals of these species were found in LS fires, suggesting that LS fires enhanced their dominance in the immediate postfire vegetation by not fully consuming their deeply buried reproductive organs. Our results suggest that LS fires significantly affected long-term understory composition development, with an apparent

In most eastern Canadian boreal forest landscapes, fire frequency has been decreasing since the end of the Little Ice Age (~ 1850) (Bergeron et al. 2004b). Moreover, simulations using the Canadian General Atmospheric Circulation Model suggest that the fire cycle may continue to increase for the decades to come (Flannigan et al. 2001, Bergeron et al. 2004a). As global climate change (GCC) may induce a longer fire cycle, this landscape may also be more susceptible to the passage of LS fires that only partially consume the thick forest floor that has accumulated during the long fire-free periods (Foster 1985). The combined effect of lower fire frequency and higher occurrence of LS fires may result at the landscape scale in fewer dense coniferous stands with an understory dominated by feathermosses, and an increase in the frequency of open coniferous stands with an understory dominated by *Sphagnum* species. If feathermoss-dominated stands are a greater source of carbon that *Sphagnum*-dominated stands (O'Connell et al. 2003), GCC may shift eastern Canadian boreal landscapes from a source to a sink of carbon in the future. This trend may be accentuated by current logging practices that protect the thick forest floor present in cut-blocks, resembling the effects of LS fires. Studies should be undertaken to establish if similar stand types (based on overstory and understory composition) but differing with respect to fire severity and/or interval show similar or different net C fluxes with respect to the atmosphere.

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Table 4.1

Summary statistics of the canonical correspondence analysis (CCA) with a forward selection of environmental variables using the chronosequence dataset.

Variable	% of variance explained	*F*	*p*
Fire severity	6	3.15	**0.02**
Fire severity * TSF[1]	6	3.50	**0.02**
TSF	6	3.45	**0.03**
Initial composition	3	1.83	0.06
Slope index	3	1.45	0.20
Mineral soil clay content	2	1.42	0.18
Initial composition * TSF	2	1.14	0.42

[1] Time since last fire

Boldface *p*-values are significant at the 0.05 level

Table 4.2

General linear model with initial composition, fire severity and time since fire as factors ($N = 42$) for the abundance of the 5 main understory taxa using the medium term (< 250 yrs) chronosequence dataset.

Variables	Source	F	p
Feathermosses	Initial composition (COMP)	-	N.S.
$R^2 = 0.23$	Fire severity (SEV)	9.03	**0.005**
	Time since fire (TSF)	4.97	**0.032**
	COMP * TSF	-	N.S.
	SEV * TSF	-	N.S.
	TSF * TSF	-	N.S.
Sphagnum spp.	Initial composition (COMP)	-	N.S.
$R^2 = 0.42$	Fire severity (SEV)	1.66	0.206
	Time since fire (TSF)	16.57	**0.0002**
	COMP * TSF	-	N.S.
	SEV * TSF	9.77	**0.003**
	TSF * TSF	-	N.S.
Cladina spp.	Initial composition (COMP)	-	N.S.
$R^2 = 0.24$	Fire severity (SEV)	9.21	**0.004**
	Time since fire (TSF)	5.90	**0.0199**
	COMP * TSF	-	N.S.
	SEV * TSF	6.36	**0.016**
	TSF * TSF	-	N.S.
L. groenlandicum	Initial composition (COMP)	-	N.S.
$R^2 = 0.34$	Fire severity (SEV)	11.84	**0.0014**
	Time since fire (TSF)	12.02	**0.0013**
	COMP * TSF	-	N.S.
	SEV * TSF	-	N.S.
	TSF * TSF	-	N.S.
Vaccinium spp.	Initial composition (COMP)	-	N.S.
$R^2 = 0.28$	Fire severity (SEV)	12.07	**0.0013**
	Time since fire (TSF)	1.24	0.2721
	COMP * TSF	-	N.S.
	SEV * TSF	5.99	**0.0191**
	TSF * TSF	-	N.S.

Boldface p-values are significant at the 0.05 level.

4.9 Figure legends

Figure 4.1: Canonical Correspondence Analysis of understory species composition using the chronosequence dataset. In A) species and explanatory variables, in B) *P. banksiana* stands and *P. mariana* stands established after high severity (HS) fires and in C) *P. mariana* stands established after high and low severity fires. In B) and C), stands are represented as average scores of stands per age-class and 1 standard deviation confidence ellipses, (light dash ,< 100 years, light line, 100 - 250 years, and thick line, > 250 years). Successional vectors connect youngest to oldest age-class for each chronosequence. In C, the successional vector of *P. mariana* stands from HS fires is shown for comparison. Environmental variables are as follows: TSF, time since last fire; SEV, centroid of stands originating after high severity fires; TotLBA basal area of large stems (dbh > 10 cm) and TotOM, total thickness of forest floor organic matter.

Figure 4.2: Abundance of five main understory taxa in relation to time since the last fire using the medium term (< 250 yrs) chronosequence dataset. A) Feathermosses (*Pleurozium schreberi and Ptilium crista-castrensis*), B) *Sphagnum spp.*, C) *Cladina spp.*, D) *Ledum groenlandicum*, E) *Vaccinium spp.*. (*V. angustifolium* and *V. myrtilloides*). The regression line for HS stands is common to both *P. mariana* and *P. banksiana* because composition effect was not significant ($\alpha = 0.05$).

Figure 4.3: Abundance of five main understory taxa in *P. mariana* stands evolving after high severity fires in relation to the extended absence of fire using the long-term (> 250 yrs) chronosequence dataset. A) Feathermosses (*Pleurozium schreberi and Ptilium crista-castrensis*), B) *Sphagnum spp.*, C) *Cladina spp.*, D) *Ledum groenlandicum*, E) *Vaccinium spp.* (*V. angustifolium* and *V. myrtilloides*). For comparative purposes the abundance values of taxa in stands evolving after LS fires are shown.

Figure 4.4: Successional pathways of ground species (boxes) as deduced from transition probabilities (arrows) in plant macrofossils found in soil organic matter profiles. For each graph, bottom row shows species that never replaced another one and top row shows species that were never replaced by another one. Middle row shows species that both replaced and were replaced. For clarity, only probabilities > 20% are shown. Sphg = *Sphagnum* spp.; Fmos = feathermosses (*Pleurozium shreberi*, *Ptilium crista-castrensis* and *Hylocomium splendens*); Poly = Polytrichum spp., Dicr = Dicranum spp.; Lich = Lichens; Wood = Dead wood.

Figure 4.1

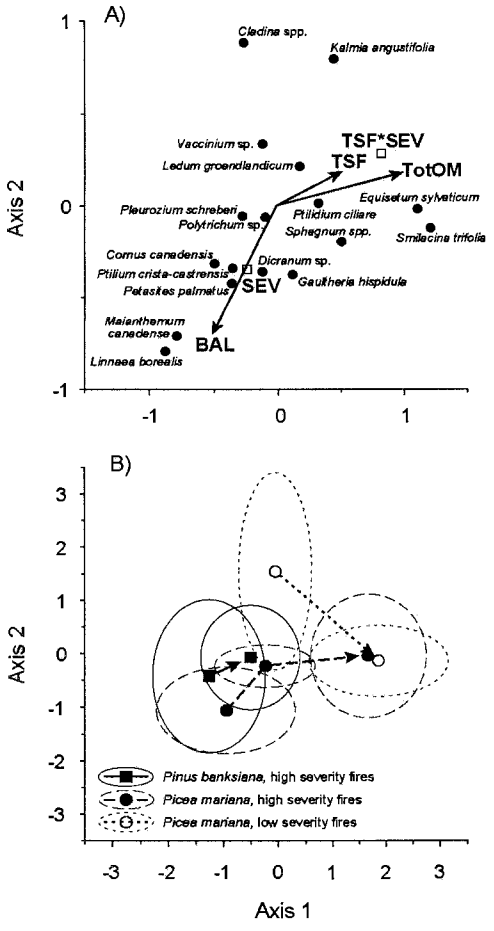

A)
Cladina spp.
Kalmia angustifolia
Vaccinium sp.
TSF*SEV
TSF
TotOM
Ledum groendlandicum
Equisetum sylvaticum
Pleurozium schreberi
Ptilidium ciliare
Polytrichum sp.
Sphagnum spp.
Smilacina trifolia
Cornus canadensis
Dicranum sp.
Ptilium crista-castrensis
Gaultheria hispidula
Petasites palmetus
SEV
Maianthemum canadense
BAL
Linnaea borealis
Axis 2
B)
Pinus banksiana, high severity fires
Picea mariana, high severity fires
Picea mariana, low severity fires
Axis 1

Figure 4.2

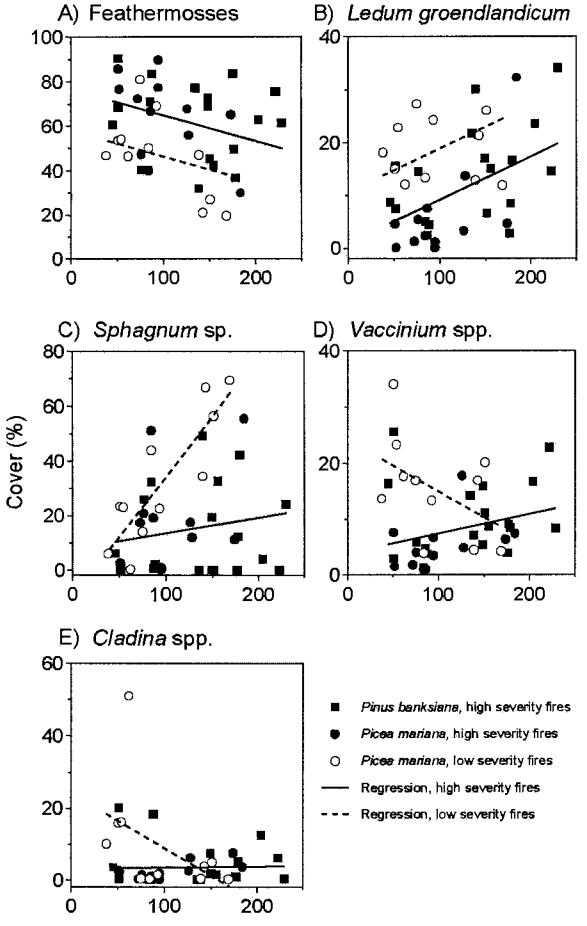

A) Feathermosses
B) Ledum groendlandicum
C) Sphagnum sp.
D) Vaccinium spp.
E) Cladina spp.
Cover (%)
Time since last fire (years)
Pinus banksiana, high severity fires
Picea mariana, high severity fires
Picea mariana, low severity fires
Regression, high severity fires
Regression, low severity fires

Figure 4.3

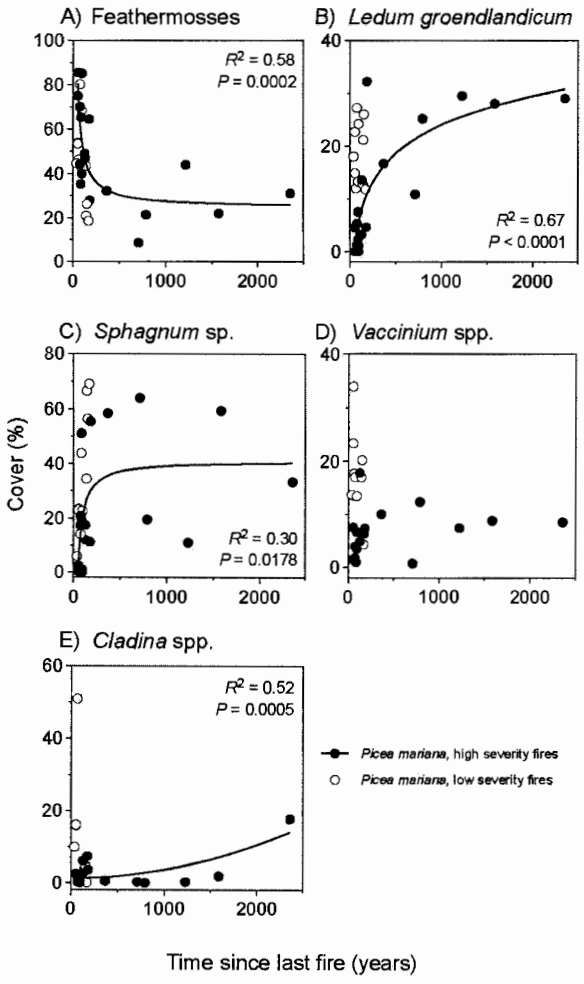
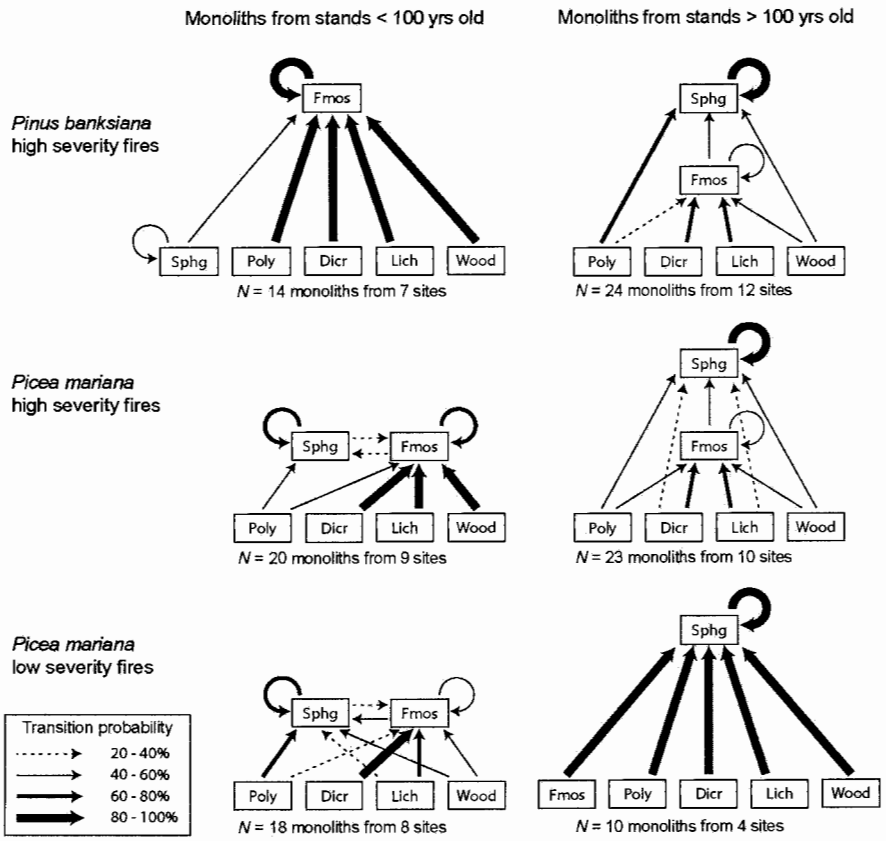

A) Feathermosses
R^2 = 0.58
P = 0.0002
B) *Ledum groendlandicum*
R^2 = 0.67
P < 0.0001
C) *Sphagnum* sp.
R^2 = 0.30
P = 0.0178
D) *Vaccinium* spp.
E) *Cladina* spp.
R^2 = 0.52
P = 0.0005
Cover (%)
Time since last fire (years)
Picea mariana, high severity fires
Picea mariana, low severity fires

Figure 4.4


Monoliths from stands < 100 yrs old
Monoliths from stands > 100 yrs old
Pinus banksiana
high severity fires
Fmos
Sphg
Poly
Dicr
Lich
Wood
N = 14 monoliths from 7 sites
N = 24 monoliths from 12 sites
Picea mariana
high severity fires
N = 20 monoliths from 9 sites
N = 23 monoliths from 10 sites
Picea mariana
low severity fires
Transition probability
20 - 40%
40 - 60%
60 - 80%
80 - 100%
N = 18 monoliths from 8 sites
N = 10 monoliths from 4 sites

Appendix 4.A

Characteristics of the chronosequence survey stands.

Site	Initial composition[1]	*P. banksiana* basal area[2] (m^{-2} ha^{-1})	Fire severity[3]	Residual OM[4] (cm)	Stand age (years)			Mineral soil			Slope Index[8]
					Oldest tree[5]	Calibrated ^{14}C age (charcoal)[6]	Calibrated ^{14}C age (humus)[7]	%sand	%silt	%clay	
30	*Pinus*	29.6	High	1.2	45	-	-	1.5	22.0	76.5	1.0
54	*Pinus*	48.2	High	1.0	51	-	-	0.0	12.7	87.3	1.9
61	*Pinus*	32.1	High	1.5	51	-	-	6.5	21.5	72.0	5.1
36	*Pinus*	39.4	High	1.6	76	-	-	1.0	23.6	75.4	0.6
38	*Pinus*	22.3	High	1.6	84	-	-	0.0	9.0	91.0	0.7
23	*Pinus*	32.0	High	1.3	86	-	-	3.5	26.9	69.7	1.4
57	*Pinus*	34.3	High	1.2	88	-	-	13.0	45.5	41.5	1.2
29	*Pinus*	40.0	High	1.2	135	-	-	19.9	30.8	49.3	1.2
69	*Pinus*	34.0	High	1.1	139	-	-	2.0	34.3	63.7	1.9
66	*Pinus*	28.5	High	1.7	149	-	-	12.5	25.0	62.5	8.7
73	*Pinus*	50.9	High	1.3	149	-	-	26.0	25.0	49.0	1.5
40	*Pinus*	35.6	High	1.1	151	-	-	25.5	27.5	47.0	2.4
49	*Pinus*	28.4	High	1.2	155	-	-	14.0	63.0	23.0	2.1
94	*Pinus*	44.7	High	1.0	176	-	-	6.0	24.5	69.5	5.1
83	*Pinus*	40.0	High	1.0	177	-	-	4.0	20.0	76.0	1.0
79	*Pinus*	20.2	High	1.1	179	-	-	2.4	29.0	68.6	0.0
65	*Pinus*	32.9	High	2.1	204	-	-	14.0	32.5	53.5	0.8
64	*Pinus*	25.8	High	1.9	222	-	-	0.0	38.4	61.6	3.9
67	*Pinus*	10.6	High	1.0	229	-	-	0.0	28.6	71.4	1.4
62	*Picea*	0.0	High	1.4	51	-	-	2.0	23.4	74.6	10.5
4	*Picea*	0.0	High	2.5	52	-	-	0.0	38.1	61.9	2.5
59	*Picea*	7.9	High	2.3	72	-	-	13.0	22.5	64.5	1.7
15	*Picea*	2.4	High	1.5	76	-	-	10.3	27.9	61.8	-4.6
2	*Picea*	0.0	High	1.9	84	-	-	0.0	21.0	79.0	0.6
56	*Picea*	0.0	High	1.3	86	-	-	13.5	28.5	58.0	0.8
12	*Picea*	0.0	High	1.1	95	-	-	0.0	20.9	79.1	2.1
55	*Picea*	0.1	High	2.5	95	-	-	14.5	30.0	55.5	0.9
18	*Picea*	0.0	High	2.0	126	-	-	15.0	18.0	67.0	1.8
75	*Picea*	0.0	High	2.0	128	-	-	3.4	24.5	72.1	-1.3
8	*Picea*	0.0	High	1.4	174	-	-	9.0	25.5	65.5	1.4
95	*Picea*	0.0	High	1.3	184	-	-	3.0	26.0	71.0	1.7
9	*Picea*	0.0	High	1.5	215	1225	-	11.5	23.5	65.0	1.6
7	*Picea*	0.0	High	1.7	217	790	-	7.5	27.0	65.5	1.1
50	*Picea*	0.0	High	2.0	222	365	-	19.0	27.0	54.0	1.3
6	*Picea*	0.0	High	3.2	280	710	555	1.0	22.7	76.4	0.4
16	*Picea*	0.0	High	2.7	286	1585	705	10.0	18.0	72.0	0.5
20	*Picea*	0.0	High	3.2	353	2355	-	5.9	22.8	71.3	1.9
11	*Picea*	0.0	Low	12.0	38	-	-	21.0	29.5	49.5	1.1
74	*Picea*	0.0	Low	13.0	51	-	-	6.0	26.5	67.5	1.3
53	*Picea*	0.0	Low	7.3	54	-	-	20.0	31.0	49.0	0.6
58	*Picea*	0.0	Low	5.8	62	-	-	23.0	30.5	46.5	2.1
78	*Picea*	0.0	Low	17.9	75	-	-	17.0	28.0	55.0	0.6
3	*Picea*	0.0	Low	16.2	93	-	-	1.9	16.0	82.0	0.0
60	*Picea*	0.0	Low	6.7	97	-	-	9.0	15.0	76.0	1.2
68	*Picea*	1.6	Low	4.6	139	-	-	1.0	22.7	76.4	0.8
63	*Picea*	0.0	Low	7.9	143	-	-	2.0	18.5	79.5	0.8
17	*Picea*	0.0	Low	17.3	151	-	-	17.5	33.0	49.5	0.8
5	*Picea*	0.0	Low	8.4	169	-	-	13.9	47.6	38.5	0.3

[1] Initial stand composition determined from the composition of dead and live trees (see Appendix 4.B) *Pinus* = *Pinus banksiana*, *Picea* = *Picea mariana*..

[2] Basal area of live and dead *P. banksiana* stems > 2 m in height

[3] Fire severity determined from the thickness of the residual organic matter (see Appendix 4.B).

[4] Thickness of the residual organic matter, *i.e.*, the organic matter that was not burned by the last fire, located between the mineral horizon and the uppermost charcoal layer.

[5] Stand age determined from tree-ring analysis. Stands where the postfire cohort of trees was not found were given a minimum age and were radiocarbon dated.

[6] Radiocarbon dates obtained for carbonised plant remains (see Appendix 4.B).

[7] Radiocarbon dates obtained for humus accumulated just above uppermost charcoal layer (from Cyr et al. 2005).

[8] Slope Index integrates slope incline and landform shape, and can assume positive (mounds or regular slopes) and negative values (depressions) (see Appendix 4.B).

Appendix 4.B

Detailed methodology used in this study

4.B.1 Stand selection and vegetation sampling

Using a stand initiation map developed for the northern part of the Clay Belt (Bergeron et al. 2004b), we visited all the burned areas located < 2 km from a road during the summers of 2000-2002. We sampled 43 distinct fires. In each fire, we visually estimated the density and composition of the postfire tree composition based on living and/or deadwood trees. If within a burned area different postfire densities and tree compositions were observed, several stands were sampled. Each stand was on fine-textured mineral deposits, on a slight incline and free of any sign of anthropogenic disturbance. Within each burned area, at least one stand (10 x 10 m quadrat) was selected for detailed dendroecological analysis. In each stand, the diameter at breast height (dbh) of all live and dead stems > 2 m in height were measured. Dead trees buried under the organic matter were exhumed and measured. According to the basal area of live and dead trees, 19 of the 48 sampled stands were dominated by *Pinus banksiana* after fire (Appendix 4.A). For the remaining 29 stands, no significant traces of any other tree species apart from *Picea mariana* were so these stands were all classified as being dominated by *Picea mariana* after fire.

At each stand, understory vegetation was described in ten 1-m^2 square plots located every 2 m along two randomly chosen 10-m transects. The cover of each species was estimated as a vertical projection of its above-ground live biomass on the forest floor.

4.B.2 Soil texture and topography

Although the mineral soil textures were hand-checked *in situ*, two mineral soil samples were taken at the centre of each stand, one at the surface and another at a depth of 1 m. Soil texture was then determined with the Bouyoucos hydrometer method (McKeague 1976). The mineral soil micro-topography, which may be masked by peat accumulation, was assessed with a theodolite in each stand along four 50-m transects each starting at the centre of the stand and passing through one of the corners. Significance of the slopes were assessed with simple linear regressions and non-significant slopes ($P > 0.05$) were given a value of zero. If the slopes of transects going in opposite directions were of opposite signs, or one or both of the slopes was null, we

calculated the slope of the two transects combined (i.e., one transect of 100 m). If the slopes were of the same sign, we summed these slopes to obtain a negative slope value (depression) or positive value (mound or incline) for the 100 m transect. The Slope Index used in this study is the mean of the slopes of the two 10-m transects.

4.B.3 Stand age determination

Stand age (fire year) was obtained by carefully dating cross-sections taken at the base of live or dead dominant trees. Cross-sections were finely sanded and crossdated using a frost-ring chronology (M. Simard, unpublished data), under a dissecting microscope at 40x magnification. Frost rings show one or several rows of distorted cells caused by growing season frosts (Bailey, 1925; Glerum & Farrar, 1966), and provide robust pointer years for crossdating. Crossdating was verified using the program COFECHA (Holmes 1983). In stands where the oldest tree exceeded 200 years, and no fire scars or pioneer species (*Pinus banksiana*) were present, samples of carbonised plant remains found in the uppermost charcoal layer within the humus profile were sent to IsoTrace Laboratories (Toronto) for AMS (Accelerator Mass Spectrometry) radiocarbon dating. As to minimise the effect of the age of the carbonised plant remain on the determination of stand age we have exclusively dated short-lived material (needles, cone scales and twigs). The radiocarbon years were calibrated in calendar years using INTCAL98 (Stuiver et al. 1998) and are shown in Appendix 4.A, along with additional radiocarbon datings from a parallel study (Cyr et al. 2005) undertaken in two of the very old stands (> 250 years). However, Cyr et al. (2005) dated the organic matter located just above the uppermost charcoal layer in the soil, which may account for their younger dates as compared to our radiocarbon dates from carbonised material. In both cases the radiocarbon dates of humus predate the age of the oldest tree present so we have used the dates obtained from carbonised plant remains.

4.B.4 Organic matter monoliths

To determine if the mosaic of successional communities observed across the landscape provided analogues for the temporal sequence at individual stands, in all 48 chronosequence stands, two to four, 10 by 10 cm monoliths of the organic layer were cut down to the mineral soil with a Wardenaar sampler (Wardenaar, 1987). The monoliths were frozen and then sliced into 1-cm sections. Subsamples of 50 cm^3 were defloculated in a 2% NaOH solution for 24 h at 60°C before a gentle manual water spray was used to

sieve the samples successively through 2 mm, 1 mm and 0.25 mm mesh. Samples were then bleached in a 10-20% HCl solution and examined microscopically at 40x magnification for identification of macroremains. The mineral soil / organic matter interface of each monolith was established where the mineral soil represented less than 25% of the sample. Individual plant remains were identified by type (cone scales, leaf fragments, seeds, etc.) and to species, genus or family depending on extent of decomposition. With respect to all macroremains present, the relative abundance of each plant remain type was then quantified (0-12.5%, 12.5-25%, 25-50%, 50-75%, 75-100%).

4.B.5 Fire severity

Charcoal fragments were extracted from each monolith slice, dried and weighed. The thickness of the postfire residual organic matter (i.e., not consumed by the last fire) was established as the number of 1-cm layers above the mineral soil and under the last charcoal layer deposited.

In the younger black spruce stands (< 200 yrs), 2.25-m long trenches were dug about 20 cm into the mineral soil. At every 15 cm along the trench, we located the charcoal layer closest to the surface and noted its position above the mineral soil (i.e., the residual organic matter thickness). Additionally, at each *P. banksiana* stand, ten and, at each *P. mariana* stand, fifteen 25 x 25 cm pits were dug into the mineral soil every 2 m along two or three 10-m transects. For each pit we noted the same measurements as for the trenches.

The severity of the last fire for each stand was qualified as high (HS) or low (LS) based on the average thickness of the residual organic matter obtained from the monoliths and from the pits and trenches. Ideally, soil burn severity is quantified as the amount of organic matter consumed (*sensu* Myanishi & Johnson, 2002). Nonetheless, as it is impossible to know how much organic matter was present in the pre-fire stand, we have chosen to qualify fire severity as the amount of organic matter not consumed by the fire (*sensu* Nguyen-Xuan *et al.,* 2000). A study of seven burns in the boreal forest has demonstrated that coniferous postfire seed germination was significantly impacted when residual organic matter approached 5 cm (Greene 2004). We used this ecologically significant threshold (5 cm) to classify soil burn severity. Among the stands sampled, 11 of the 29 *P. mariana* stands were established after the passage of a LS fire (Appendix 4.A).

4.B.7 References

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Appendix 4.C

Frequency and mean cover of the 17 taxa present in over 10% of the 1 m^2 plots for each chronosequence

	Frequency (% of plots)				Mean cover (%)			
	Chronosequence				Chronosequence			
Understory species	*Pinus banksiana* HS fire	*Picea mariana* HS fire	*Picea mariana* LS fire	All stands	*Pinus banksiana* HS fire	*Picea mariana* HS fire	*Picea mariana* LS fire	All stands
Pleurozium schreberi	93.7	91.6	92.7	92.7	54.8	46.4	45.3	49.4
Sphagnum spp.	29.5	60.0	71.8	50.8	13.2	26.5	32.6	22.7
Ledum groenlandicum	71.6	66.8	87.3	73.3	14	11.4	18.6	14.0
Vaccinium spp.	88.9	64.2	90.0	79.6	10.2	5.9	15.4	9.7
Cladina spp.	41.1	35.3	60.9	43.3	4.2	2.6	9.4	4.8
Ptilium crista-castrensis	37.4	33.2	19.1	31.6	6.3	5.2	1.4	4.8
Gaultheria hispidula	46.8	70.5	55.5	58.0	3.3	6.2	1.9	4.1
Kalmia angustifolia	13.2	28.9	56.4	29.0	1.4	2.1	7.5	3.1
Cornus canadensis	63.2	30.0	24.5	41.6	3.4	1.0	0.6	1.9
Equisetum sylvaticum	12.6	27.4	33.6	23.1	0.3	1.9	3.9	1.7
Ptilidium ciliare	29.5	26.3	12.7	24.5	1.5	1.8	0.3	1.4
Dicranum spp.	47.4	49.5	30.9	44.5	1.3	1.8	0.6	1.3
Polytrichum spp.	16.3	21.6	31.8	21.8	0.8	0.6	1.0	0.8
Petasites palmatus	26.8	6.3	6.4	14.3	1.2	0.4	0.2	0.7
Linnaea borealis	23.7	6.8	0	11.8	1.3	0.3	0	0.6
Smilacina trifolia	2.6	16.8	13.6	10.6	0	0.7	0.6	0.4
Maianthemum canadense	24.2	3.2	0	10.6	0.5	0.1	0	0.3

Appendix 4.D

Transition probabilities of ground species and dead wood from one (1-cm thick) soil horizon (below in profile, or previous in time) to the next (above in profile, or following in time) using macrofossil data from soil organic matter profiles. Data is shown for the three chronosequences under study: PBA HS = *Pinus banksiana* after high severity fire, PMA HS = *Picea mariana* after high severity fires, and PMA LS = *Picea mariana* after low severity fires; and per age classification.

		Replacing species (above in monolith)														
		Monoliths from all stands					**Monoliths from stands < 100 yrs**						**Monoliths from stands > 100 yrs**				
PBA - HS		*N* = 38 monoliths from 19 stands					*N* = 14 monoliths from 7 stands						*N* = 24 monoliths from 12 stands				
		Sphg	Fmos	Poly	Dicr	Lich		Sphg	Fmos	Poly	Dicr	Lich		Sphg	Fmos	Poly	Dicr	Lich
Species or dead wood (below in monolith)	Sphg[b] (35%)[a]	0.89	0.09	0.01	0	0.01	Sphg (2%)	0.52	0.43	0	0	0.05	Sphg (43%)	0.92	0.07	0.01	0	0.01
	Fmos[c] (22%)	0.29	0.66	0	0.02	0.03	Fmos (40%)	0.01	0.93	0	0	0.06	Fmos (17%)	0.45	0.5	0.01	0.03	0.02
	Poly[d] (1%)	0.52	0.44	0.02	0	0.02	Poly (1%)	0	0.98	0.01	0	0.02	Poly (1%)	0.65	0.31	0.02	0	0.02
	Dicr[e] (< 1%)	0.06	0.86	0.01	0.07	0.01	Dicr (< 1%)	0	0.98	0	0.01	0.01	Dicr (< 1%)	0.09	0.78	0.02	0.1	0
	Lich[f] (< 1%)	0.09	0.77	0	0.04	0.1	Lich (1%)	0	0.81	0	0	0.18	Lich (< 1%)	0.16	0.73	0	0.06	0.04
	Wood[g] (3%)	0.3	0.66	0	0.01	0.03	Wood (1%)	0.08	0.91	0	0	0	Wood (3%)	0.4	0.54	0	0.02	0.04
PMA - HS		*N* = 43 monoliths from 19 stands					*N* = 20 monoliths from 9 stands						*N* = 23 monoliths from 10 stands				
		Sphg	Fmos	Poly	Dicr	Lich		Sphg	Fmos	Poly	Dicr	Lich		Sphg	Fmos	Poly	Dicr	Lich
	Sphg (38%)	0.79	0.21	0	0	0	Sphg (18%)	0.62	0.36	0.01	0	0	Sphg (47%)	0.88	0.12	0	0	0
	Fmos (11%)	0.38	0.59	0	0.02	0.01	Fmos (20%)	0.2	0.77	0	0.03	0	Fmos (7%)	0.54	0.44	0	0.01	0.01
	Poly (< 1%)	0.48	0.46	0.05	0.01	0	Poly (< 1%)	0.47	0.47	0.05	0	0	Poly (< 1%)	0.54	0.41	0.02	0.04	0
	Dicrn (< 1%)	0.18	0.73	0	0.08	0	Dicr (< 1%)	0.01	0.86	0	0.13	0	Dicr (< 1%)	0.33	0.63	0.01	0.03	0
	Lich (< 1%)	0.18	0.76	0	0.01	0.05	Lich (< 1%)	0	0.98	0	0	0.02	Lich (< 1%)	0.22	0.71	0	0.01	0.06
	Wood (7%)	0.37	0.61	0	0.01	0.01	Wood (7%)	0.19	0.81	0	0	0	Wood (7%)	0.51	0.45	0	0.01	0.02
PMA - LS		*N* = 28 monoliths from 12 stands					*N* = 18 monoliths from 8 stands						*N* = 10 monoliths from 4 standss				
		Sphg	Fmos	Poly	Dicr	Lich		Sphg	Fmos	Poly	Dicr	Lich		Sphg	Fmos	Poly	Dicr	Lich
	Sphg (42%)	0.79	0.18	0.03	0	0	Sphg (37%)	0.69	0.26	0.04	0	0	Sphg (51%)	0.95	0.04	0.01	0	0
	Fmos (7%)	0.53	0.39	0.03	0	0.05	Fmos (9%)	0.4	0.5	0.03	0	0.07	Fmos (5%)	0.8	0.19	0.02	0	0
	Poly (< 1%)	0.75	0.19	0.06	0	0.01	Poly (< 1%)	0.71	0.22	0.06	0	0.01	Poly (< 1%)	0.84	0.11	0.05	0	0
	Dicr (< 1%)	0.49	0.49	0	0.01	0	Dicr (< 1%)	0.01	0.97	0	0.02	0	Dicr (< 1%)	0.98	0.02	0	0	0
	Lich (< 1%)	0.35	0.55	0	0	0.1	Lich (< 1%)	0.25	0.63	0	0	0.11	Lich (< 1%)	0.96	0.02	0	0	0.01
	Wood (5%)	0.63	0.31	0.01	0	0.06	Wood (7%)	0.5	0.4	0	0	0.09	Wood (2%)	0.85	0.14	0.01	0	0

C[a] Mean abundance in macrofossil samples

[b] Sphg = *Sphagnum* spp.

[c] Fmos = Feathermosses (*Pleurozium schreberi*, *Hylocomium splendens*, and *Ptilium crista-castrensis*).

[d] Poly = *Polytrichum* spp.

[e] Dicr = *Dicranum* spp.

[f] Lich = Lichens

[g] Wood = Dead wood

CONCLUSION GÉNÉRALE

C.1 Dynamique des peuplements au sein du domaine de la pessière de l'Ouest.

Au sein du domaine de la pessière de l'Ouest, nous retrouvons sur les dépôts de surface des fréquences différentes de composition après feu mais aussi des trajectoires successionelles différentes. Notre étude suggère que le potentiel d'entourbement des différents dépôts de surface exercerait une influence sur le régime des feux et la trajectoire des peuplements qui s'installent après feu. Les changements de structure des peuplements coïncident avec les changements de composition. Par contre, en comparant la structure des jeunes et vieux peuplements dominés par l'épinette noire, nos résultats indiquent que des changements de structure en absence du feu peuvent avoir lieu même sans changement dans la composition. Par ailleurs, au sein des jeunes classes d'âge, la variabilité de la structure et la composition des peuplements suggèrent que d'autres paramètres du feu (notamment la sévérité du dernier feu), en dehors du temps écoulé depuis le dernier feu, pourraient être importants pour expliquer la diversité de peuplements au sein de ce paysage particulièrement en terme de structure. Toutefois, l'absence prolongée du feu engendre une convergence des peuplements vers des peuplements dominés par l'épinette noire et caractérisés par une canopée ouverte.

C.2 La dynamique des peuplements conifériens sur dépôts fins

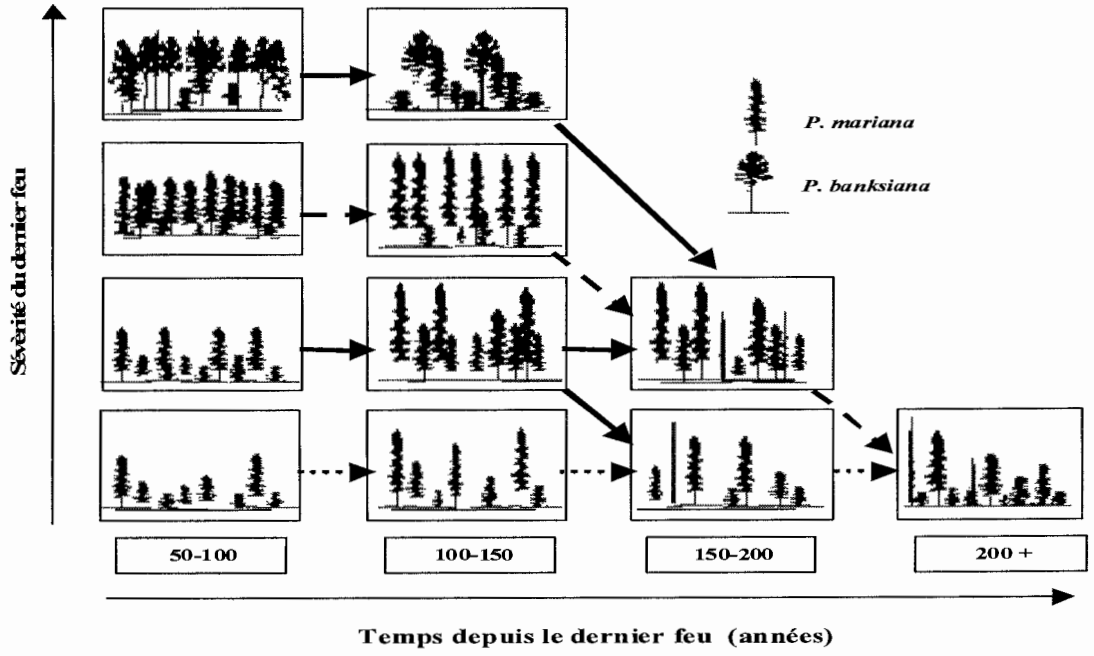
Notre étude de chronoséquence, qui a pris en compte la sévérité du dernier feu et la composition après feu, confirme qu'en absence prolongée du feu (>100 ans) *P. banksiana* est graduellement remplacé par le *P. mariana*. Toutefois, la composition après feu sévère (*Pinus* vs *Picea*) a eu peu d'effet sur l'évolution de la structure des peuplements (Chapitre 2), l'accumulation de matière organique (Chapitre 3) ou la composition de sous bois (Chapitre 4).

Après un feu sévère, une régénération abondante entraîne une fermeture rapide de la canopée et un sous bois dominé par les mousses hypnacées. En l'absence prolongée du feu, les perturbations secondaires (Harper et al. 2002) entraînent une ouverture de la canopée. Cela induit des changements de composition considérable dans la strate muscinale et arbustive avec notamment, une augmentation importante de la couverture du

Ledum groenlandicum et un remplacement des mousses hypnacées par les sphaignes. L'accumulation constante de la matière organique à travers le temps, associée à une augmentation dans la couverture de sphaignes et de *L. groenlandicum,* diminue la croissance des arbres ce qui empêche une refermeture de la canopée (Heinselman, 1963, Glebov and Korzukhin 1992) (Figure C.1).

Figure C.1 :

Dynamique des peuplements en fonction du temps depuis le dernier feu et la sévérité du dernier feu



La sévérité du feu influence grandement l'évolution de la structure des peuplements (Chapitre 2), l'accumulation de la matière organique (Chapitre 3) et la composition de sous bois (Chapitre 4). La présence de matière organique diminue la régénération après feu et la croissance subséquente de semis. La faible régénération après feu et la présence de matière organique empêche la fermeture de la canopée et entraîne un envahissement précoce par les sphaignes et *L. groenlandicum* (Figure C.1).

Il s'ensuit qu'en l'absence prolongée du feu, peu importe la composition après feu ou la sévérité du dernier feu, nous observons dans ce paysage une convergence des peuplements établis après feu vers des peuplements d'épinette noire avec une canopée ouverte, un sous bois dominé par les sphaignes et une épaisse couche de matière organique accumulée au sol (Figure C.1).

L'étude de la stratigraphie des macrorestes au sein de la matière organique accumulée au sol a révélé les mêmes tendances par rapport à l'évolution de la composition de sous bois que l'approche de chronoséquence (Chapitre 4) ce qui valide nos séries évolutives et renforce les résultats obtenus avec l'approche utilisant une chronoséquence (Chapitre 2,3).

C.3 Aménagement écosystémique des peuplements conifériens sur dépôt fin

Nous observons trois types de perturbations en pessière : certaines entraînent un vieillissement des peuplements, d'autres rajeunissent à différent degrés les peuplements. Ces perturbations naturelles se distinguent par leurs effets sur la canopée et sur la matière organique accumulée au sol. En absence de feu, le vieillissement des peuplements est entraîné par des perturbations secondaires (chablis, épidémies d'insectes, sénescence, etc.) qui ouvrent partiellement la canopée tout en ayant peu d'effet sur la matière organique accumulée au sol. Quoique les feux en général entraînent une ouverture complète de la canopée, certains consomment entièrement la matière organique au sol (feu sévère) alors que d'autres ne la consomment que partiellement (feu peu sévère).

Tableau C.1 :

Comparaison des effets des perturbations naturelles et quelques approches sylvicoles sur la canopée et la matière organique accumulée au sol.

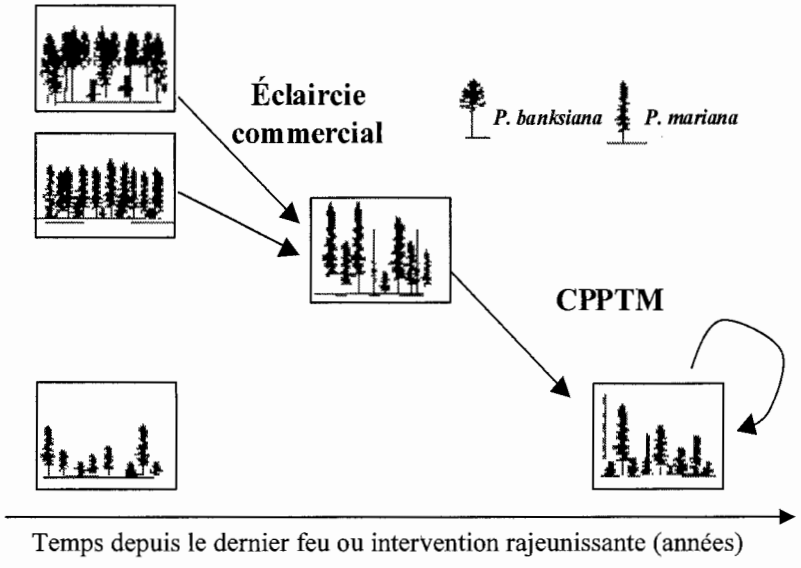
	Effet sur la canopée	Effet sur la matière organique accumulée au sol	Interventions sylvicoles avec effets semblables
A. Perturbations naturelles qui rajeunissent le peuplement			
Feu sévère	Ouverture complète	Consommation complète	Rajeunissement intensif : Coupe totale suivi de brûlage dirigé / préparation mécanique et plantation à haute densité
Feu peu sévère	Ouverture complète	Consommation partielle	Échec du rajeunissement intensif
B. Perturbations naturelles qui vieillissent le peuplement			
Chablis Épidémies	Ouverture partielle	Peu d'effet	Vieillissement : coupes partielles
C. Interventions sylvicoles préconisée actuellement			
Coupe avec protection des sols et de la régénération (CPRS)	Ouverture complète	Peu d'effet	-

Actuellement au Québec, il se pratique presque exclusivement des Coupes avec Protection des Sols et de la Régénération (CPRS). En récoltant toutes les tiges

marchandes, cette intervention sylvicole engendre l'ouverture complète de la canopée et, par définition, a peu d'effet sur la matière organique accumulée au sol. Puisque les effets des CPRS ne ressemblent pas aux effets des principales perturbations opérant sur ce territoire (Tableau C.1), nous croyons que cette pratique pourrait être abandonnée lorsqu'il est question d'interventions sur dépôts fins en pessière. En remplacement, nous proposons un aménagement basé sur la dynamique forestière et composé de deux types d'approches sylvicoles: des approches qui vieillissent les peuplements et d'autres qui les rajeunissent. De plus, nous préconisons une valorisation des échecs occasionnels de régénération suite aux interventions rajeunissantes.

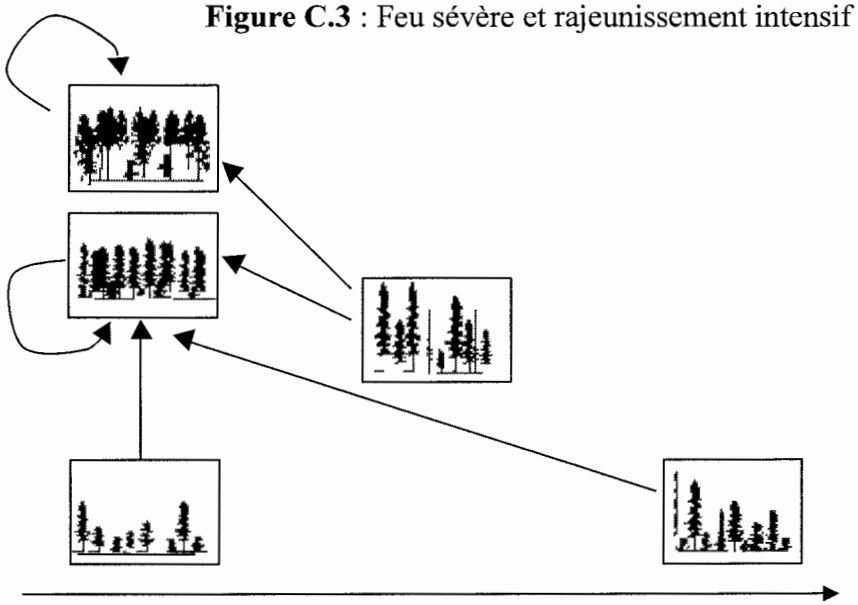
Nous proposons de faire évoluer des peuplements denses et réguliers issus de feux sévères vers des peuplements plus irrégulier en se servant d'éclaircies commerciales et puis d'ouvrir davantage ou de maintenir l'ouverture des peuplements avec l'application de coupes avec protection des petites tiges marchandes (CPPTM) (Figure C.2). Toutefois étant donné l'age moyen des peuplements et l'importance du processus d'entourbement dans ce secteur (Boudreault et al. 2002; Bergeron et al. 2004a; Chapitre 3) des peuplements entourbés caractéristiques des forêts de fin de succession sont très présents dans ce territoire sous l'appellation 'improductif'. Donc l'application des coupes partielles devrait y être limitée.

Figure C.2 : Perturbations secondaires et les coupes partielles



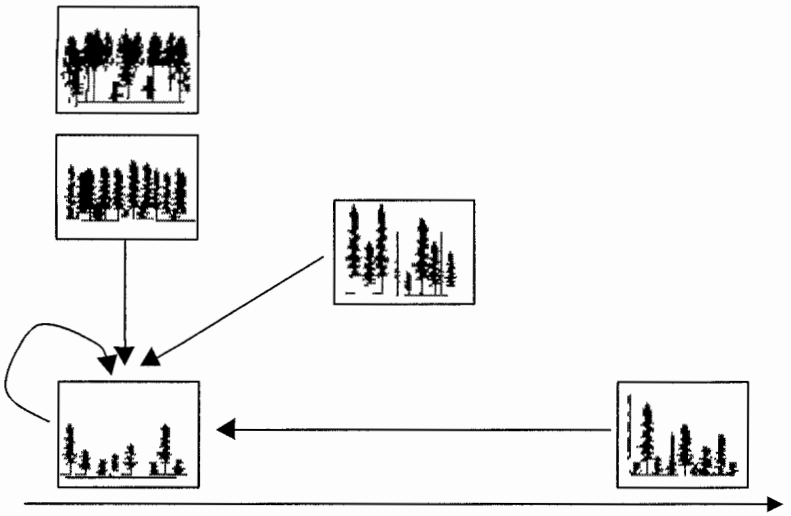
Pour rajeunir l'ensemble des peuplements nous proposons une approche intensive qui s'inspire des effets d'un feu sévère et donc ouvre complètement la canopée (coupe totale), élimine la matière organique au sol (brûlage dirigé, préparation mécanique) et est suivie par une régénération abondante pour favoriser la fermeture de la canopée (plantation à haute densité : 4000-5000 tiges) (Figure C.3).

Figure C.3 : Feu sévère et rajeunissement intensif



Étant donné les nombreux facteurs qui peuvent influencer le succès de la régénération (broutage, gel, sécheresse), nous proposons de mettre en valeur les échecs de rajeunissement en se servant de la dynamique de ces peuplements comme analogue à la dynamique suite à des feux peu sévères naturels (Figure C.4). Nous suggérons donc de tenter d'installer des peuplements denses et productifs dans tous les parterres de coupes rajeunissantes, sachant très bien qu'il y aura des échecs de régénération qui ont toutefois une valeur écologique étant donné l'importance au sein de ce territoire des échecs de régénération suite à des feux peu sévère.

Figure C.4 : Feu peu sévère et échec de rajeunissement intensif



Le choix de la méthode à appliquer devrait prendre en compte les résultats de l'étude présentée en Annexe 1 qui suggèrent que le processus de paludification (accumulation de matière organique) est fortement influencé par la présence de sphaignes et d'éricacées. La composition de sous-bois pourrait, en indiquant le degré de paludification des peuplements, aider à choisir le type d'intervention à appliquer. Des peuplements démontrant des degrés élevés de paludification devraient être rajeunis de manière intensive (remise en production). Puisque des peuplements démontrant des degrés de paludification faible (couverture faible d'éricacées, de sphaignes, fine couche organique accumulée au sol) possèdent encore un potentiel productif intéressant, ces peuplements seraient plus propices à l'application d'interventions qui les vieillissent.

C.4 L'aménagement écosystémique et la société civile.

La fréquence d'application des différents types d'interventions devrait prendre en compte la variabilité naturelle de la fréquence des feux dans ce territoire qui a varié entre 50-500 ans pendant l'Holocène (Carcailler et al. 2000). Les écologues forestiers sont à même de jouer un rôle essentiel à ce niveau en décrivant une gamme de variabilité naturelle; le défi consiste en fait à choisir au sein de cette variabilité la cible de proportion de chaque type de peuplement que nous souhaitons conserver au sein du territoire. Ce choix relève d'un choix de société alors surtout lorsqu'une part importante de la forêt est publique, comme c'est le cas de notre site d'étude. À ce titre, les gestionnaires devront préconiser des modes de gestion qui font une large place à la société civile et aux

différents intérêts reliés à la forêt ce qui est conforme à une définition plus englobante de l'aménagement écosystémique (Grumier, 1997; Corner and Moite 1999). Les récentes initiatives entreprises dans les provinces en matière de participation publique à la confection des plans d'aménagement sont encourageantes en ce sens. Or, les différences entre les approches du Québec, de Terre-Neuve et de l'Ontario, révèlent combien il reste à faire au Québec pour améliorer l'ouverture du processus décisionnel à la société civile et rendre plus significatif le rôle du citoyen dans les prises de décisions associée à la mise en place d'un aménagement écosystémique et à l'atteinte du développement durable (Annexe 2).

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ANNEXE I

Participatory requirements in forest management planning in Eastern Canada: a temporal and interprovincial perspective

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AI.1 Abstract

With the introduction of the concept of sustainable forest management, the practice of public participation has become omnipresent. This study focuses on provincial participatory requirements in forest management planning (FMP). A comparative framework composed of four participatory process attributes (power, moment of participation, learning/interaction, and procedure) was used to obtain a temporal and interprovincial perspective of Quebec's new participatory process. Our results indicate that with respect to past processes Quebec's current approach allows certain stakeholders but not the general public to have more access to FMP. Comparatively, Ontario and Newfoundland have implemented different, clearly stated, approaches that involve the general public at numerous stages of FMP. Future research should concentrate on how these participatory requirements are implemented and on the public satisfaction with regard to this implementation.

Key words: Public participation, forest management planning, descriptive framework, Canada, Quebec, sustainable forest management.

AI.2 Résumé

Exigences participatives reliées aux plans d'aménagement forestier dans l'est du Canada : une perspective temporelle et interprovinciale.

La participation du public est devenue un incontournable avec l'introduction du concept de développement forestier durable. Notre étude s'intéresse aux processus de participation publique provinciaux reliés à l'élaboration des plans d'aménagement forestier sur terres publiques et aux exigences légales qui les précèdent. Une analyse comparative de l'approche québécoise actuelle a été effectuée en utilisant un cadre descriptif composé de quatre dimensions d'analyse (pouvoir, moment de la participation, apprentissage/interaction et procédure); celle-ci a été comparée avec ses précédents dispositifs et avec ceux de deux provinces voisines (Terre-Neuve et Ontario). Les résultats indiquent une ouverture du processus décisionnel à de nouveaux acteurs quoiqu'elle soit restreinte à certains groupes d'intérêt plutôt qu'au 'grand public'. Les approches retenues par les provinces voisines se distinguent par les occasions multiples qu'elles offrent au 'grand public' de prendre part au processus décisionnel relié aux plans. Les études futures devraient explorer la façon dont ces exigences règlementaires sont appliquées et le niveau de satisfaction des participants à l'égard de ces mécanismes.

Mots-clés: Participation du public, plans d'aménagement forestier, cadre d'analyse descriptif, forêts publiques, Canada, Québec, gestion forestière durable.

AI.3 Introduction

During the 1990s, provincial decision–makers in Canada adopted the concept of sustainable forest management (SFM) in the context of forest management planning (FMP). This has redefined the public's role in FMP. Indeed, public participation (PP) is now an integral component of provincial legislation and SFM criteria-and-indicators systems (e.g., Canadian Council of Forest Ministers 2003, Newfoundland Forest Service 1995). Although there is considerable work on this topic (e.g., Blouin 1998; Duinker 1998), to date there is no systematic description and comparison of the different provincial PP approaches in FMP that highlights the similarities and differences between the provinces. However, we believe that future PP approaches can benefit from current and past experience. This paper focuses mainly on Quebec, where the new millennium has been characterized by many changes to PP (Government of Quebec 2001). It describes the effects of recent legislative changes on PP in FMP. A comparative approach was used to obtain a temporal and inter-provincial perspective on Quebec's new participatory approach, which was contrasted with both its previous requirements and current ones in Ontario and Newfoundland. These provinces were chosen because of their geographical proximity, similar tenure systems and hierarchy of management plans and because the majority of their commercial public forests are situated within the eastern boreal biome.

AI.4 Comparative Framework

Our study focuses on the provincial legislative requirements pertaining to PP in FMP in public forests under forest tenure. Inspired by the PP literature (e.g., Beirle 1998, Blahna and Yonts-Shepard 1989, Daniels and Walker 1996, Konisky and Beirle 2001), process-level traits, which are reasonably easy to qualify, were chosen to develop a comparative framework composed of four "Participatory Process Attributes" (PPAs): power, moment of participation, learning interaction and procedure. Based on an analysis of the literature and government documents, different provincial participatory requirements were qualified and compared with the PPAs, an approach resembling that of

Del Furia and Wallace-Jones (1998) and the Organization for Economic Cooperation and Development (2001).

1) The *Power* PPA refers to the extent of influence citizens have on decisions associated with FMP. Participatory processes imply opening the decision-making process to actors other than traditional ones (i.e., government and industry), which implies more opportunities for "new" actors to influence decisions. To qualify the extent of the public's influence in each participatory approach, we used Arnstein's (1969) typology comprising different "levels" of participation (Table AII.1).

2) The *Moment of participation* PPA is concerned with when (timing) and how often (frequency) citizens are invited to participate in the decision-making process. For this PPA, the overall management process was divided into five stages: 1) elaboration; 2) information; 3) consultation; 4) implementation; and 5) evaluation. We qualified the "timing" of participation by identifying the stages in which the public participates. *Frequency* refers to how the public is involved in the planning stages: singular (happens once), punctuated (happens at different moments), or continuous (happens in an ongoing fashion).

3) The *Learning interaction* PPA refers to the process allowing for exchange of knowledge between participants and for communication and exchange between actors in a more interpersonal sense. It relates to the initiatives that improve everyone's mutual-trust and understanding of the range of values, interests, and concerns; for example, mechanisms that allow sustained contact between the participants (e.g., committees, field trips), or that favor the development of constructive dialogue between stakeholders (e.g., ground rules). This PPA was qualified based on three types of interactions: unilateral (from managers to participants); bilateral (from managers to participants and, from participants to managers); and active (dialogue between managers and participants). As

participatory processes often distinguish between representatives of interest groups and the general public, we have qualified the *Moment of participation* and *Learning-interaction* PPAs separately for each type of participant.

4) The *Procedure* PPA refers to how the process and its mandate are stated (unclear, clear), and pertains to the functioning of the process and the role of participants in the FMP as well as the formal and legal requirements of the participation exercise. This PPA was evaluated based on the publication of citizen guides to FMP or adherence to clearly stated, jointly approved, ground rules before FMP.

AI.5 An Temporal Perspective: History of Quebec's participatory process in FMP

Quebec's *Forest Act* was first proclaimed in 1987, and then amended in 1994 and 2001. We describe its participatory approach during three distinct periods (Table AI.2). The original *Forest Act* (1987) stated that the public must be informed of the content of management plans on public land. After the tenure holder had deposited the plan at the Ministry, the plan was available for the public to view for 45 days (during business hours at the Ministry or the tenure holder's office). The *Power* PPA was qualified as information because the public was allowed to view the draft, but was not consulted or able to comment on it. Furthermore, participation occurred only at the information stage (stage 2) and the public was involved only once, after the plan was formulated. The flow of information during this process was unidirectional, i.e., from the beneficiary to the public, and there were few opportunities for the public to interact with the ministry, the beneficiary or each other, thus, there was no interpersonal exchange. This simple participatory process was clearly defined in the *Forest Act*.

The 1994 *Forest Act* amendments introduced few changes to Quebec's participatory process (Table AI.2). However, the public was given the opportunity to comment on the draft (written comment within the first 20 days of the information period), and municipal representatives now had to be personally consulted by tenure holders. A conciliation procedure was also introduced: if there was a conflict, the district manager named a conciliator who had 10 days to resolve it. The public was now involved

at specific moments during two stages of the planning process: information and consultation (stages 2 and 3). Although this approach fell near the consultation rung on the ladder of citizen participation, as it occurred very late in the planning process, it could hardly be considered "real consultation" (Tanz and Howard 1990), thus, it fell between the Information and Consultation levels. Furthermore, although the comment and conflict-resolution period did allow some opportunity for bilateral exchange of substantive knowledge, there was virtually no face-to-face contact between the different stakeholders, and thus, little opportunity for relationship building. As in the original *Forest Act,* the participatory process to be undertaken was clearly defined.

The 2001 *Forest Act* amendments increased the comment and conflict-resolution periods from 20 to 25 days and from 10 to 20 days, respectively, although the information period remained 45 days. The fundamental change is the adoption of article 54, which states that local interest groups, but not necessarily the general public, must be invited to participate in the development phase of FMP. Specific interest groups are mentioned (municipalities, h unters, o utfitters, n ative c ommunities), b ut t he d oor i s l eft open to invite other organizations or individuals. Although the general public may still participate during the information and consultation phases (stages 2 and 3), representatives are now involved earlier and continuously from the beginning of the planning process until the final tabling of the plan (stages 1, 2, and 3). Quebec's new participatory approach resembles Arnstein's (1969) placation strategy of participation, where "a few hand-picked worthy individuals are placed on public bodies." With representatives involved earlier, there are more opportunities for active exchange of knowledge and interpersonal contact among some, but not all, stakeholders (exclusion of the general public in the elaboration stage). Finally, as the recently amended *Forest Act* does not mention what type of process should be used or define the role of the tenure holder, the Ministry representatives or the general public in FMP, the process and mandate of this approach remain unclear.

AI.6 An Interprovincial Perspective: Ontario's and Newfoundland's Participatory Processes in FMP

In Ontario, the Ministry of Natural Resources' (OMNR) Class Environmental Assessment for Timber Management on Crown Lands (Government of Ontario 1994) requires that the Ministry establish a Local Citizens Committee (LCC) for each management unit (OMNR 1998). The LCC represents local interests, such as business, hunters, the tourism industry, naturalists, municipalities, native groups, etc. One member of the LCC can be a voting member on the planning team (which includes foresters, fish and wildlife biologists, forest ecologists, and park and fire specialists). LCC members have continuous access to all stages of the process, and the general public is invited to participate at five distinct times during the first three stages, i.e., at the beginning of the planning phase until deposit of the final plan. Anyone that is unsatisfied may suggest another course of action by writing to the plan's author, who will meet with the person to try to resolve the issue. The MNR District Manager has the final say; if anyone is dissatisfied with the decision, they may ask the Minister of Environment and Energy for an environmental assessment of specific forest management activities identified in the plan. Although Ontario's approach is different than Quebec's current process, it also resembles Arnstein's Placation level of participation. The LCCs and the five stages including PP create an opportunity for forestry professionals and the general public to meet, and learn about different forestry-related issues and values (Duinker 1998). Finally, OMNR's *Guide to Forest Management Planning* (1998) clearly defines the conflict-resolution process, public involvement, and when participation is solicited.

In Newfoundland, the Ministry of Forest Resources and Agrifoods is mandated to include the public in FMP through joint-planning teams for each management district (except in three districts fully allocated to Abitibi-Consolidated, L. Moores, pers. comm.) (Newfoundland Forest Service 1995). Conflict resolution follows 11 principles of consensus, with a scale of 8 levels of agreement (Department of Forest Resources and Agrifoods 2005a). However, the district ecosystem manager or tenure holder retain the right to write the plan if consensus cannot be reached. Additionally, as anyone can become a member, joint-planning teams allow universal access to the process and, since joint planning teams mutate into joint monitoring teams when the planning process is

finished, the public is continuously involved throughout all stages of the planning process (Nazir and Moores 2001). Newfoundland's PP requirements correspond to Arnstein's (1969) partnership strategy of PP, which is described as a process where "power is redistributed through negotiation between citizens and power holders as they agree to share planning and decision-making through such structures as joint planning boards or committees." Joint planning teams offer stakeholders and the general public the opportunity to get to know each other and create an environment primed for active dialogue and deliberation (with some districts having field trips and bi-monthly meetings) (Moores and Duinker 1998). The conflict-resolution process, planning-team representation, and principles of conduct are all clearly stated in the ground rules at the beginning of the process, and these rules can be modified at any time during the process.

AI.7 Discussion

Our results indicate that from a temporal perspective the impacts of the recent legislative changes on public participation in forest management in Quebec have been numerous with notably an earlier involvement of representatives in the process and better opportunities for an active exchange of knowledge between the various stakeholders. However, in comparison to its neighbors, Quebec's current participatory approach differs with respect to several dimensions of public participation in forest management planning.

In Quebec the general public's involvement is limited to after the draft plan is deposited and until the plan is approved, while in Ontario the general public is involved during the elaboration stage and in Newfoundland during all stages of the planning exercise. Moreover, the involvement of representatives in Quebec ends when the final plan is approved while in the two other provinces they are continuously involved during the implementation and evaluation stages. Finally, while its neighbors have clearly stated how and when participatory processes will be undertaken, Quebec has remained, nearly four years since the passage of the last *Forestry Act* amendments, ambiguous on this facet of participation.

Quebec's current approach is encouraging; including representatives earlier in the process should give certain citizens more influence in decision making, and promote opportunities for the active exchange of knowledge and relationship building. Yet there

are still some shortcomings, notably regarding the extent of the general public's involvement and the clarity of the mandate and process. As Ontario and Newfoundland have implemented different, clearly stated, participatory approaches that involve the general public at numerous stages of FMP, Quebec may have something to learn from its neighbors about how and when to involve the public in FMP.

AI.8 Conclusion

Our study constitutes a first level of analysis as it focuses on some key attributes of the formal requirements regarding PP in FMP. Future studies should explore additional dimensions but also how these requirements are implemented in the actual practice of PP. The entity that organizes and controls the participatory exercise could be an important attribute to incorporate in future comparisons. In Ontario and Newfoundland the Ministry has taken the lead in organizing and chairing public participation processes. Comparatively in Quebec, the government has bequeathed this responsibility to the forest industry. If both Ontario and Newfoundland operate under a more rigid framework which does not permit a diversification of participatory processes, on the other hand, Quebec's approach has brought about an undertaking of a variety of different types of PP mechanisms (Nadeau *et al.* 2004). While Quebec's approach may facilitate the capacity of participatory processes to adapt to local peculiarities, the delegation of responsibility to the forest industry may engender some conflict of interest, as the forest industry is also an important stakeholder.

Future studies should also analyze participant satisfaction with the implementation of participatory requirements as it is an essential component of the new criteria and indicators system of SFM (Canadian Council of Forest Ministers 2003). Some studies have already indicated that participants in all three provinces are concerned about the representativity of committees and their degree of influence in FMP (Moores and Duinker 1998, OMNR 2002, Nadeau *et al.* 2004). Eventually, the correlation between the structure of a public participatory process and the public's satisfaction of this process and its outcomes should be understood. This would enable the identification of the multiple dimensions that characterize a socially desirable PP process in FMP and

yield suggestions on how provinces can improve their respective participatory practices as they strive to attain SFM.

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Table AI.1

Eight rungs on a ladder of citizen participation used to qualify the Power VPA (adapted from Arnstein, 1969).

8. Citizen Control	Degrees of citizen power
7. Delegated Power	
6. Partnership	
5. Placation	Degrees of citizen influence
4. Consultation	
3. Information	
2. Therapy	Non participatory
1. Manipulation	

Table AI.2

Qualification of the provincial participatory requirements with respect to four participatory process attributes (see text for explanation).

Participatory Process Attributes				Provincial Processes				
				Quebec 1987-1993	Quebec 1993-2001	Quebec since 2001	Ontario	Newfoundland
1.	Devolution of Power			Information	Consultation / Information	Placation	Placation	Partnership
2.	Moment of participation	Representatives	*Timing*	2	2,3	1,2,3	1,2,3,4,5	1,2,3,4,5
			Frequency	Singular	Singular	Continuous	Continuous	Continuous
		Public	*Timing*	2	2,3	2,3	1,2,3,4,5	1,2,3,4,5
			Frequency	Singular	Singular	Singular	Punctuated	Continuous
3.	Learning interaction	Representatives		Unilateral	Bilateral	Active	Active	Active
		Public		Unilateral	Bilateral	Bilateral	Active	Active
4.	Procedure			Clear	Clear	Unclear	Clear	Clear